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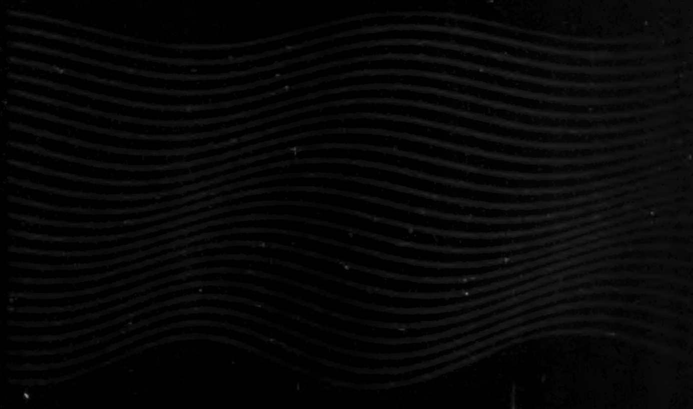

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Design: Ludvic Saleh & Associates, Ottawa
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Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 51, No. 5, May 1994

Volume 51, n° 5, mai 1994

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Reproductive Tactics of Walleye (*Stizostedion vitreum*) in Lake Erie[1]

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Henderson, B.A., and S.J. Nepszy. 1994. Reproductive tactics of walleye (*Stizostedion vitreum*) in Lake Erie. Can. J. Fish. Aquat. Sci. 51: 986–997.

The average age of mature female walleye (*Stizostedion vitreum*) (5 yr) assessed in October or November is about 1 yr younger than the average age of spawners (6 yr) collected in April of the next year. To determine why there was a delay in the age at first reproduction, walleye were collected in western Lake Erie and the Thames River. Energy stored in the form of fat increased exponentially with body weight. Gonad size increased linearly with body size, the ovary constituting a relatively constant 18–22% of total body weight over all body sizes. Although allometric relations constrain energy acquistion and allocation, ecological conditions (water temperature and prey availability) affect variability within those bounds. Surplus energy (stored energy minus energy allocated to gonads and metabolism) was increasingly available for females greater than 2 kg, corresponding to females older than 5 yr. Thus, age at first reproduction is influenced by the physiological constraints on acquiring and allocating energy and by the energetic demands of spawning. Energetic condition of the spawning stock was associated with year-class strength. The strong 1991 year-class was produced by females with greater surplus energy than the spawners of the weak 1992 year-class.

L'âge moyen de dorés (*Stizostedion vitreum*) femelles matures (5 ans) examinées en octobre ou en novembre (avec des ovules développés dans l'ovaire) devance d'environ un an l'âge moyen des génitrices (6 ans) capturées en avril de l'année suivante. Afin de déterminer la raison de cet écart dans l'âge de la première ponte, des dorés ont été prélevés dans la partie ouest du lac Érié et dans la rivière Thames. L'énergie accumulée sous forme de tissus adipeux s'accroît exponentiellement avec le poids. La taille des gonades s'accroît de manière linéaire avec la taille des sujets; l'ovaire correspond de manière assez constante à une proportion de 18 à 22 % de la masse totale de l'organisme, peu importe les classes de taille. Même si des relations allométriques limitent l'acquisition et la répartition de l'énergie, il reste que les conditions écologiques (température de l'eau et disponibilité des proies) agissent sur la variabilité à l'intérieur des limites. Le surcroît d'énergie (énergie stockée moins énergie attribuée aux gonades et au métabolisme) est de plus en plus disponible pour les femelles qui pèsent plus de 2 kg; il s'agit de la classe des femelles de plus de 5 ans. Ainsi, l'âge des femelles à leur première ponte est influencé par les contraintes physiologiques liées à l'acquisition et à l'attribution de l'énergie, ainsi que par les demandes en énergie de la ponte. Le bilan énergétique du stock géniteur a été associé à l'importance des classes d'âge. L'importante classe d'âge de 1991 a été produite par des femelles qui disposaient d'un surplus énergétique plus important que celui des génitrices de la peu importante classe d'âge de 1992.

Received July 19, 1993
Accepted December 8, 1993
(JC013)

Reçu le 19 juillet 1993
Accepté le 8 décembre 1993

Recruitment is the single most important factor affecting yield of walleye (*Stizostedion vitreum*) to the commercial and angling fishery in Lake Erie (Nepszy 1977). Environmental conditions (water temperatures and storms) prevailing during the spawning period have been associated with variations in recruitment (Busch et al. 1975). Parental stock size explained only a small part of the variation in recruitment (Shuter and Koonce 1977). An important assumption of the management protocol of walleye in Lake Erie is that recruitment is largely unpredictable and unrelated to the abundance of spawning females.

Identification of the spawning population is usually a problem. Not surprisingly, the best demonstration of a relation between stock and recruitment is found when measurement error of both stock size and recruitment is small (Ricker 1954; Walters and Ludwig 1981). Except for most anadromous species, one estimates the size of the spawning stock by multiplying the proportion mature at age or size by the corresponding abundance in the lake. In most cases, maturity is assessed some months prior to spawning. In walleye, the presence of eggs in the ovary in the preceding autumn or summer is taken as an indication of maturity.

Exploratory analyses of the relation between stock and recruitment of walleye in Lake Erie led us to believe that the effective spawning population may be different from the one expected from the maturation schedule. Ridgway et al. (1991) have also shown that small mature smallmouth bass (*Micropterus dolomieun*) do not spawn. A possible explanation for the discrepancy between the apparent and real reproductive potential of a population may be found in an exploration of the energetics of growth and reproduction. It is clear that fecundity and maturation are influenced by growth rates (Weatherley 1972), but the mechanism that explains the allocation of energy to growth, maintenance, and reproduction is less clear (Fisher 1958). The selective pressures that have shaped this mechanism may be associated with the costs and benefits of reproduction (Shine and Schwarzkoff 1992). The consequences or costs of reproduction may be reduced growth and survival (Hirshfield 1980; Roff 1982, 1983, 1984) or spawning in alternate seasons (Lambert and Dodson 1990).

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[1] Contribution No. 93-01 of Ontario Ministry of Natural Resources, Aquatic Ecosystem Research Section, Fisheries Policy Division, Box 5000, Maple, ON L6A 1S9, Canada.

We are concerned with the relation between the bioenergetics of walleye reproduction and recruitment of offspring to the population. Do the constraints of allocating energy reserves to reproduction or maintenance explain the discrepancy between the apparent and real maturation schedule? Does the likelihood of spawning depend on the energy reserves acquired during the preceding growing season?

Methods

Lake Erie is a large mesotrophic lake supporting a large commercial fishery for walleye, yellow perch (*Perca flavescens*), rainbow smelt (*Osmerus mordax*), and white bass (*Morone chrysops*) (Loftus et al. 1987). Our samples were taken from the western basin (area = 3300 km^2; mean depth = 7.4 m; 41°31′N, 82°30′W to 83°W) and the western portion of the central basin (area = 16 200 km^2; mean depth = 18.5 m; 41–42°39′N, 80°00′W to 82°30′W).

Chemical composition, fecundity, sex, maturity, weight, length, and age were determined for samples of mature female walleye captured in experimental and commercial gill nets in the autumn (October and November 1990, $N = 68$; December 1991, $N = 100$) and in commercial gill nets (stretch mesh >76 mm) in the spring (April 1991, $N = 94$; April 1992, $N = 70$). We assume that the population sampled in the autumn consisted of walleye that were both mature and immature; in contrast, in the spring, we were sampling mature females from a population that may have segregated into mature and immature individuals. For the samples taken in the autumn, the total body (gonads and somatic tissue combined) chemical composition (lipid, protein, water) was assayed whereas in the spring, separate chemical analyses were done on the gonads and somatic tissue.

Experimental gill nets consisted of 13 mesh sizes of 30.5-m panels each arranged in a random order (114-, 57-, 95-, 51-, 89-, 108-, 64-, 121-, 76-, 127-, 70-, 102-, 83-mm stretched mesh) and the last two mesh sizes (38 and 44 mm) with 13.7-m panels. Although two different sampling gears were used to collect mature females, selectivity would not significantly affect the age-classes caught because large mature females are caught mainly in mesh sizes greater than or equal to 76 mm in both experimental and commercial gear. A sample of mature ascending females was collected in seines during March (1992) from the mouth of the Thames River flowing into Lake St. Clair. Experimental gill nets were set annually in the western and west-central basins from 1978 to 1991 in October and November (Henderson and Wong 1991). From these catches, we estimated the average maturity schedule for males and females over all years. The ages of all walleye sampled from the Canadian waters of Lakes Erie and St. Clair were determined from scale impressions on acetate slides.

The Ohio Department of Natural Resources (Sandusky, Ohio) sampled walleye (March and April of 1990 and 1991) from catches in seines and trapnets set near or in the Sandusky River on the southern shore of the western basin of Lake Erie. The ages of these walleye were determined from a size (total length (millimetres)) ages key (age 2 <370, age 3 >370 and <445, age 4 >445 and <500, age 5 >500 and <535, age 6 >535 and <555, age 7 >555 and <600, age 8 and older >600 mm). The size ranges at each age for walleye collected from Ohio waters of Lake Erie were derived from the samples of walleye collected from our multimesh gill nets (1978–91) in Canadian waters. The ages of these Ohio samples were, therefore, inferior in quality to our own ages determined from scales.

Fecundity was estimated by removing three 1-g subsamples from the anterior, middle, and posterior sections of the ovary and then multiplying the average number of eggs per gram (wet weight) of the three ovarian subsamples by the total wet weight of the ovary. Ovarian subsamples were preserved in either alcohol or formalin. Chemical composition (ash, protein, fat) of soma and ovaries was determined in the manner described by Elliott (1976). We determined the relative clutch mass (RCM equals mature ovary weight divided by total body weight) described by Shine and Schwarzkoff (1992); the gonadosomatic index (GSI) (Gunderson and Dygert 1988; Lenhardt 1992) is a comparable index of gonadal development applied at any stage of development.

We did not try to estimate precisely the energy budget of the walleye over winter because we did not know how much food was consumed from December to March. Metabolic data (temperature and size related) were not available for walleye, so estimates of metabolic costs were made using the formulation described by Robinson et al. (1983), but fitted with data provided by Altman and Dittmer (1974) for routine metabolism of yellow perch:

$$V_{O_2} = 0.056B^{-0.1121}e^{0.0687TC}\ (R^2 = 0.47,\ P = 0.03)$$

where C = temperature (centigrade), T = time measured (hours), V = millilitres of O_2 per gram per hour, and B = weight of walleye (grams). We assumed that the metabolic parameters of yellow perch were generally applicable to walleye (cf. Kitchell and Stewart 1977).

Calories of lipids metabolized were estimated by multiplying the number of litres of O_2 consumed by the energy relation for lipid metabolism (4.66 kcal of lipids consumed per litre of O_2 consumed; Brett and Groves 1979). Similarly, the caloric value of the lipids available before winter was estimated by multiplying the dry weight of lipids in the whole carcass by a constant (9.45 kcal per gram of lipids; Brett and Groves 1979).

We estimated the amount of energy from lipids (autumn) that would be diverted into reproductive tissue (gonads in the spring) by using the relations between fecundity and ovarian weight (grams), the proportion of lipids in ovaries (spring), and the caloric content of lipids derived from the spring samples. Here, we assumed that the potential size and energy content of undeveloped autumnal gonads could be inferred from characteristics of spring gonads, if one knew first the fecundity of both autumnal and spring ovaries and second the size and energy content of spring ovaries.

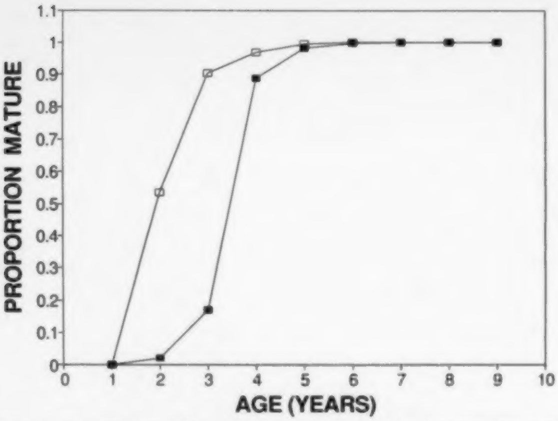

FIG. 1. Proportion of walleye mature by age in the western and central basins of Lake Erie from autumn samples (1978–88). Ages were adjusted to correspond to age in the following spring (age in the spring = age in the autumn + 1). Open squares are males and solid squares are females.

These parameters were used to predict the ratio of lipid-kilocalories in the gonads to the total (gonad and somatic) lipid-energy (RCM-lipid), should all of these females, sampled in the autumn, have spawned next spring because the gonads were not fully developed in the autumn before spawning. The weight of spring gonads was regressed on spring fecundity:

(1) $GW_s = a_sF_s + b_s$

and it was assumed that the regression parameters could be used to predict potential gonad weight in the next spring from fecundity in the previous autumn:

(2) $GW_a = a_sF_a + b_s$.

This assumption was based on our observations (described later in the results) that fecundity differed little between autumn and the following spring. The energy density of the spring gonads

(3) c_s = kilocalories per gram of spring ovary

was used to predict the potential energy content of the autumn gonads:

$$\theta_a = c_s GW_a.$$

Parameters are defined as follows: GW_s = spring gonad weight, a_s = slope of spring gonad/ fecundity, F_s = spring fecundity, b_s = intercept of spring gonad/ fecundity, GW_a = autumn gonad weight, F_a = autumn fecundity, and θ_a = energy content of autumn gonad. In contrast, the actual RCM-lipid was estimated from the carcass and gonads of walleye collected in the spring. Surplus energy was the difference between the caloric content of total lipid content measured from the autumn samples minus the predicted amount of energy allocated to the ovary and the estimated metabolic requirements at 2°C for 3–5 mo starting in December.

Indices of young-of-year abundance were obtained by trawling (10-min duration) during August in the western basin of Lake Erie. From 1980 to 1986, fixed sites ($N = 7$) were trawled repetitively in Canadian waters; since then, randomly selected stratified sites ($N = 79–141$) were trawled in both Canadian and U.S. waters. A 10-m Biloxi bottom trawl was used in all years except 1980–81 when a smaller outboard trawl was used; thus, the catches may have been smaller in 1980 and 1981 because the gear was less efficient. Catches of young-of-year were transformed by a square root of the catch per trawl.

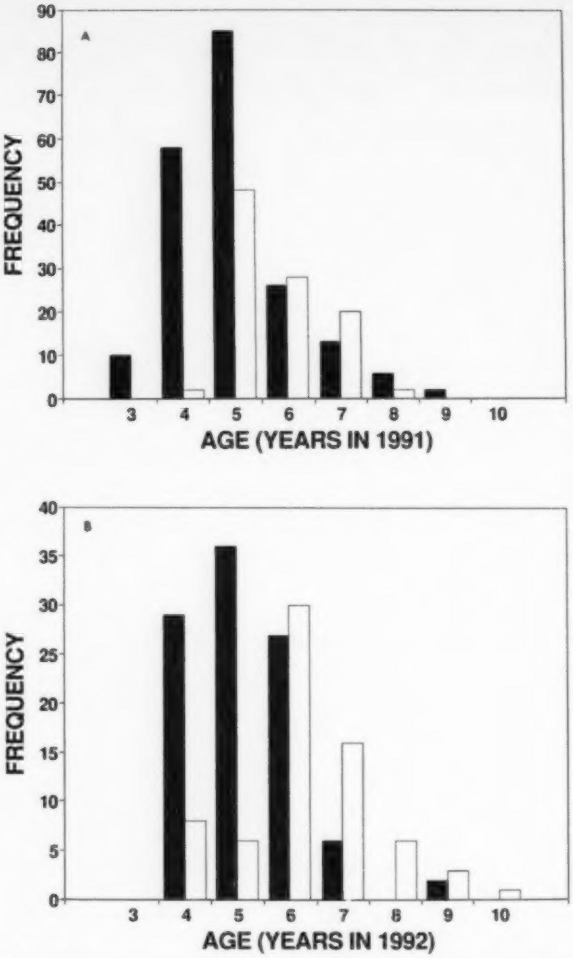

FIG. 2. Age composition of mature females determined from autumn sample (solid bars) of mature females and spring age structures (open bars) of mature females collected on or near spawning shoals in the western basin of Lake Erie in (A) 1990–91 and (B) 1991–92.

Results

Expected and Observed Age Structure of Female Spawners

From an assessment of gonadal development in October (1978–88), we found that most 4-yr-old females (in the year of spawning) and most 3-yr-old males were mature (Fig. 1); age was expressed as the age in the spring so that a female at age 3 in the autumn was described as age 4 at spawning in the spring. However, the average age of the spawning population (1991 and 1992) was greater than that predicted from the maturation schedule determined in the preceding autumn (Fig. 2).

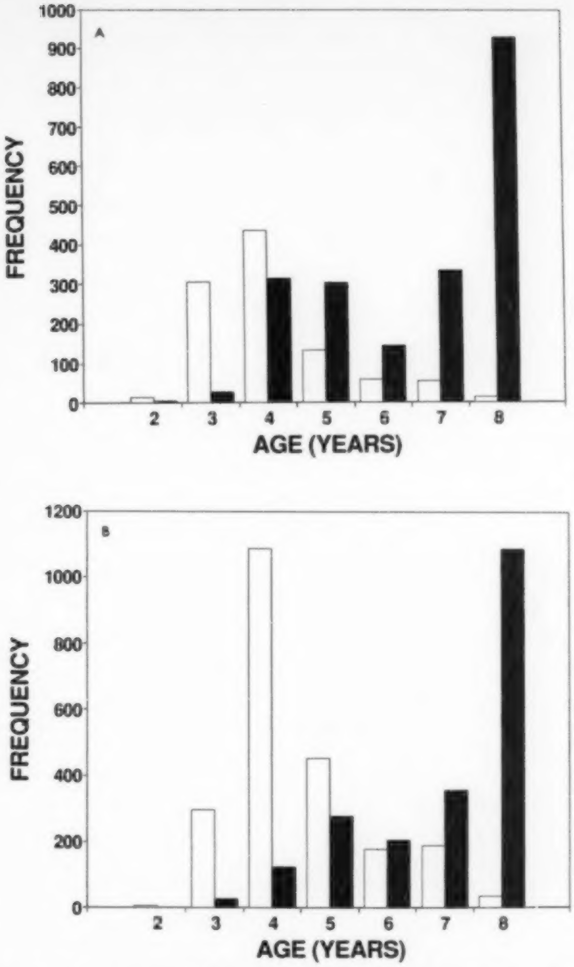

FIG. 3. Age structure of spawning males (open bars) and females (solid bars) caught in Ohio waters of the western basin of Lake Erie in March and April in (A) 1990 and (B) 1991) (data courtesy of Ohio Division of Wildlife, Lake Erie Fisheries Station, Sandusky, Ohio).

The age structure of spawning males caught in Ohio waters was consistent with the age structure predicted from the autumn sample, but the age structure of spawning females was different from the age structure of mature females sampled in the autumn (Fig. 3). The modal age of the males in 1990 was 4 yr which was consistent with the maturation schedule derived in the autumn (Fig. 1) and the strength of the 1986 year-class; the decline in the catch after age 4 was reminiscent of a typical catch curve. Despite the weakness of the 1987 year-class (4 yr old in 1991), the modal age of males was also age 4 in 1991. In contrast, the modal age of females was 8 yr and older and inconsistent with the expected age structure derived from the maturation schedule or variations in year-class strength (Fig. 1). The dominance of females aged 8 yr and older was not just an artifact of pooling all larger females greater than 600 mm (forklength); walleye older than 8 were rare in the population as a whole (Fig. 4). In summary, males seemed to be maturing as expected from the internal examination of gonadal development (Fig. 1), but females were maturing at a much greater age than expected.

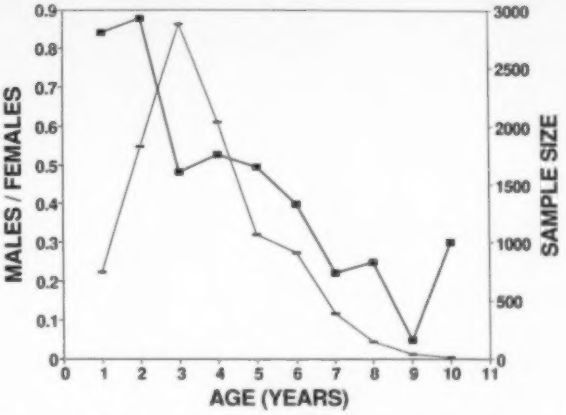

FIG. 4. Ratio of males to females (solid squares) and sample size (horizontal bars) by age-class for samples taken from commercial catches of walleye (1978–90) in Lake Erie.

The early maturation of males may be associated with higher levels of natural mortality. The ratio of males to females in the samples from the commercial fishery declined with age, with a marked decrease at age 3, coincident with the age at which most males matured first (Fig. 4). Although gill nets were selective, the size difference between sexes from ages 1 to 5 was not sufficient to explain the decrease in the proportion of males in the catch (Henderson and Wong 1991).

The discrepancy between the observed and expected age structure of the spawning population can be explained by the energetic cost of reproduction. If the maturity schedule (Fig. 1) were correct, we should be able to predict the age structure of the spawning females. Most males were mature by age 3 yr (age by following spring) and females by age 4 yr, when maturity was assessed in the autumn. However, females did not mature until age 5 so that predicted age structure was younger than the observed age structure of spawning females (Fig. 2). Although a high proportion of 4-yr-old females was assessed as mature in the autumn, based on internal inspection of gonadal development, a much smaller percentage of these 4-yr-old females spawned the next year. The age structures of mature males and females were strikingly different in the waters adjacent to or in the rivers of Ohio. In the springs of 1990 and 1991, the difference in the modal ages of Ohio's males (4 yr) and females (8 yr) was much greater than predicted by the maturation schedule. A "bimodal age composition" of spawning male and female walleye was also observed for walleye from Lake Simcoe spawning in the Talbot River (Pugsley 1983). In this population, there was an 8-yr difference between the modal ages of spawning males (4 yr) and females (12+ yr). We contend that this delay in the onset of maturity of females is a reflection of the cost of producing ovaries. In comparison, much less energy was allocated to the males' testes, and therefore, one might expect that males could mature earlier. However, although the energetic cost of producing testes is low, there may be other energetic costs associated with spawning behaviour that lead to increased mortality of males.

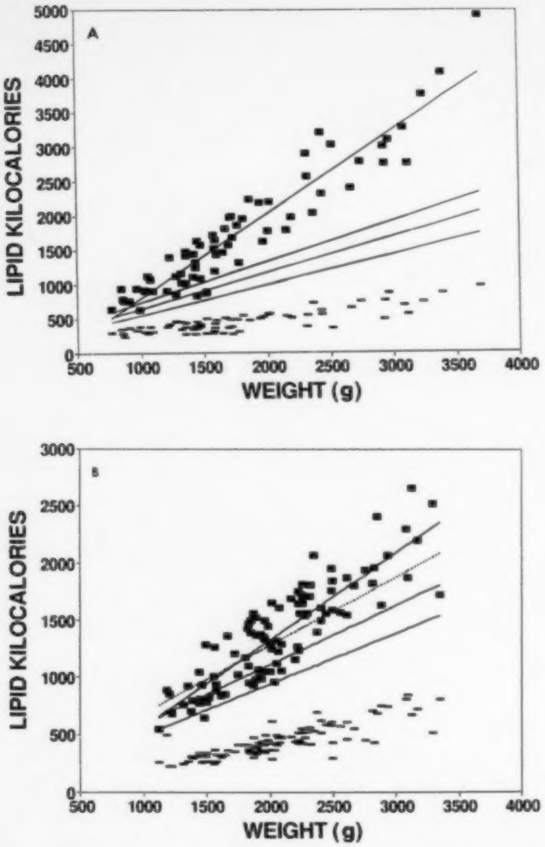

FIG. 5. Kilocalories of stored fat (solid squares), predicted consumption of lipid calories by walleye (3, 4, and 5 mo of routine metabolism at 2°C plus caloric content of ovary, three lower lines in each figure), and the predicted energy content of the ovaries (horizontal bars) during (A) 1990–91 and (B) 1991–92.

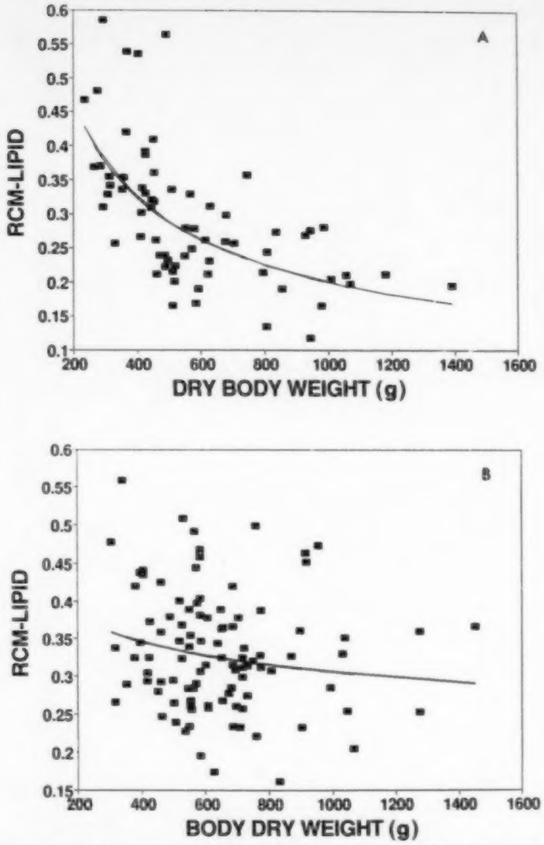

FIG. 6. Relation between the predicted ratio of lipid-kilocalories in mature ovaries to the total lipid-energy available (RCM-lipid) and dry body weight (autumn estimates) in (A) 1990–91 and (B) 1991–92.

Allocation of Reserve Energy to Reproduction

How much energy was available for reproductive tissue and could a deficiency of surplus energy constrain maturation? Kilocalories of stored lipids increased linearly with the round weight of female walleye for the autumn 1990 and 1991 samples (Fig. 5). From the equations for routine metabolism (yellow perch), we estimated caloric demand for 3, 4, and 5 mo at 2°C to show the relation between the energy reserves (kilocalories of lipids) and metabolic demands. Thus, although the total surplus energy increased with the size of the female, more energy was needed for metabolic demands, and predicted proportion of available energy allocated to reproductive tissue therefore decreased with the size of the female.

Do larger females really allocate proportionally less of their surplus energy to reproduction? In the autumn of 1990 (Fig. 6), the predicted ratio of lipid-kilocalories in the gonad to the total lipid-kilocalories in the carcass and gonads (RCM-lipids) was inversely related to body weight ($\log_e$(RCM-lipids) = $-0.5257\cdot\log_e$ (dry body weight) + 2.0221, df = 66; $r^2 = 0.42$). This regression was potentially confounded by the lack of independence between the dependent and independent variables, so the estimated gonadal lipid-calories were regressed on the total lipid-calories in the body ($\log_e$(gonadal lipid-calories) = $0.51 \pm 0.061\cdot\log_e$ (total body lipid-calories) + 2.30, $r^2 = 0.51$; $P = 0.001$). The slope of this regression was significantly less than 1.0 ($P < 0.001$), so that, by inference, the proportion of available lipid-calories allocated to gonadal tissue declines with an increase in the size of the walleye (Fig. 6). The mean RCM-lipid measured directly in the following spring (1991 = 0.29 ± 0.058 (SE = standard error)) for females with fully developed gonads corresponded to the larger females sampled in the previous autumn. For the 1991 autumn sample, the relation between RCM-lipids and body size was inverse also, but not significant ($\log_e$ (RCM-lipids) = $-0.1341\cdot\log_e$ (dry body weight) − 0.2563, df = 98; $r^2 = 0.03$). The absence of a significant inverse relation in 1991–92 was caused by an increased variability of lipid content relative to the size of females (1990–91 LK = (1.221 ± 0.0533 (SE))·RW − (422.5 ± 301.49 (SE)); 1991–92 LK = (0.7464 ± 0.0439)·RW − (201.2 ± 217.69); LK = lipid-kilocalories, RW = round weight (grams)). However, the regression of estimated gonadal lipid-calories on total body lipid-calories was significant and the slope was significantly less than 1.0 ($\log_e$(gonadal lipid-calories) = $0.71 \pm 0.062\cdot\log_e$ (total body

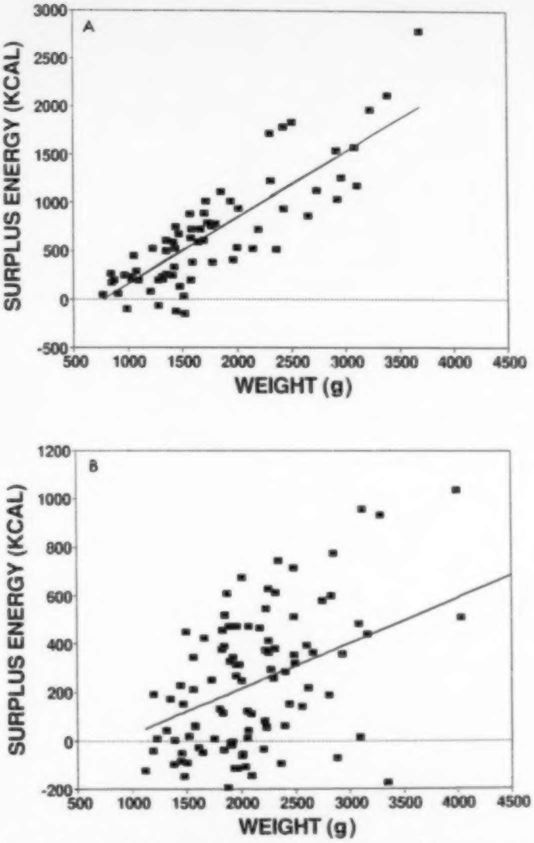

FIG. 7. Surplus lipid-energy in relation to body weight for females collected in the autumns of (A) 1990 and (B) 1991. Note that for graphical representation, the *y*-scales are different in Fig. 7A and 7B.

lipid-calories) + 0.94, $r^2 = 0.57$; $P = 0.001$; slope significantly different from 1.0, $P = 0.001$). For this year-class of spawners (autumn 1991 and spring 1992), the predicted RCM-lipid ratio was higher from the sample taken in the autumn (1991 = 0.33 ± 0.078 (SE)) than the mean RCM-lipid measured directly in the following spring (1992 = 0.26 ± 0.061 (SE)) for females with fully developed gonads. Thus, in the two years (1991 and 1992 year-classes), larger females did allocate a smaller proportion of available energy to gonadal tissue. Furthermore, it appeared that the spawners were only the larger females (weighing more than about 1800 g) with lower ratios of lipid energy allocated to reproductive tissue. These larger females also had more surplus energy (Fig. 7). The 1992 spawners had fewer and more variable surplus calories than the 1991 spawners. Thus, one would have predicted that a smaller proportion of the potential spawners (autumn) would have successfully matured by the spring in 1992 than in 1991.

The difference between potential energy stored and required (surplus energy) increased as walleye aged. The proportion of energy stored as somatic lipids was approximately constant over all ages and sizes of walleye, and therefore, the absolute amount of lipid energy increased with age and size. The range of available prey species and sizes increases with the size of walleye (Hurley 1986) as a consequence of a greater swimming speed and larger mouth whereas walleye metabolic rate declines with body size (Weatherley 1972). Therefore, one expects that surplus energy would increase with body size (Ware 1980). Apparently, the age or body size (about age 5 yr or 1800 g), at which stored energy exceeds the combined energy required for routine metabolism and ovarian tissue, corresponds to the age of maturity indicated from age composition of the spawning population. Below this size or age, stored energy was equivalent to the need, with little or no surplus. Thus, females usually, but not always, have enough energy to meet metabolic and direct reproductive costs (ovaries), but will not spawn in the absence of energy surplus to these requirements.

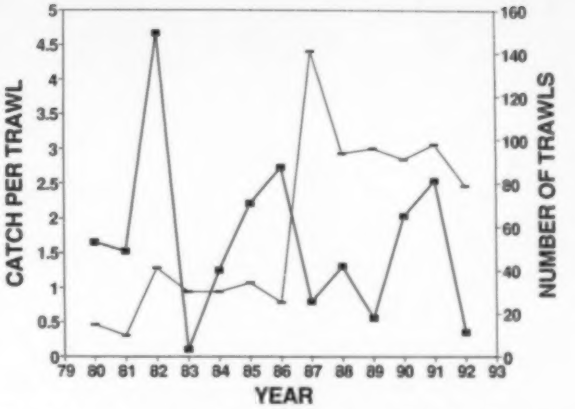

FIG. 8. Year-class strength of young-of-year walleye (solid squares; square root transformation) and number of trawls (horizontal bars) in the western basin of Lake Erie (1980–92).

Annual Recruitment of Young-of-Year

There were three relatively large year-classes from 1980 to 1992 (Fig. 8). Abundant year-classes (1982, 1986, and 1991) were followed by sparse year-classes. Catches of yearlings in gill nets set in October were consistent with our indices of year-class strength from trawl catches (Henderson and Wong 1991).

Although in a general way, surplus energy increases with the size of the walleye, there is scope for considerable variation in the ability of individual walleye to realize their potential. As seen in Fig. 7B, there was a large number of large females that had less stored energy than was necessary to meet the requirements of producing a mature ovary and meeting metabolic demands before spawning. Unless sufficient energy could be obtained just prior to spawning, these females would not spawn. We hypothesize that there is a time (February and March) just before spawning in April when the final stage of vitellogenesis occurs. Thus, we suggest that there is little opportunity for the females to improve their energetic state after the November preceding spawning in the spring of the following year, unless the winter is exceptionally mild. In comparison with the females spawning in 1991, the 1992 spawners appeared to have relatively less energy to fulfill the requirements of overwinter metabolism and ovarian development. The lipid-energy content of mature ovaries was greater in 1991 (1.34 ± 0.1374 (SE) kcal/g wet weight) than in 1992 (1.193 ± 0.1119 (SE) kcal/g

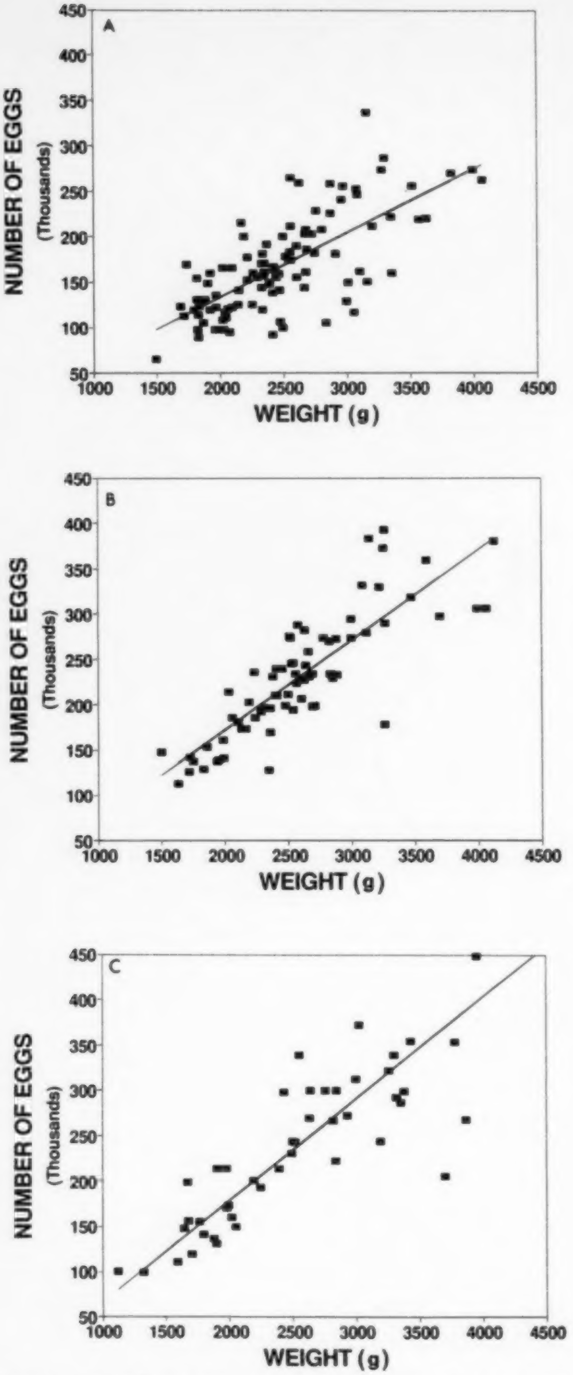

FIG. 9. Fecundity of walleye in relation to round weight from spring in (A) Lake Erie, 1991, (B) Lake Erie, 1992, and (C) Thames River, 1992.

wet weight). The poor recruitment from the 1992 spawners may have been partly explained by the energy deficiency of these spawners compared with the 1991 spawners (Fig. 8).

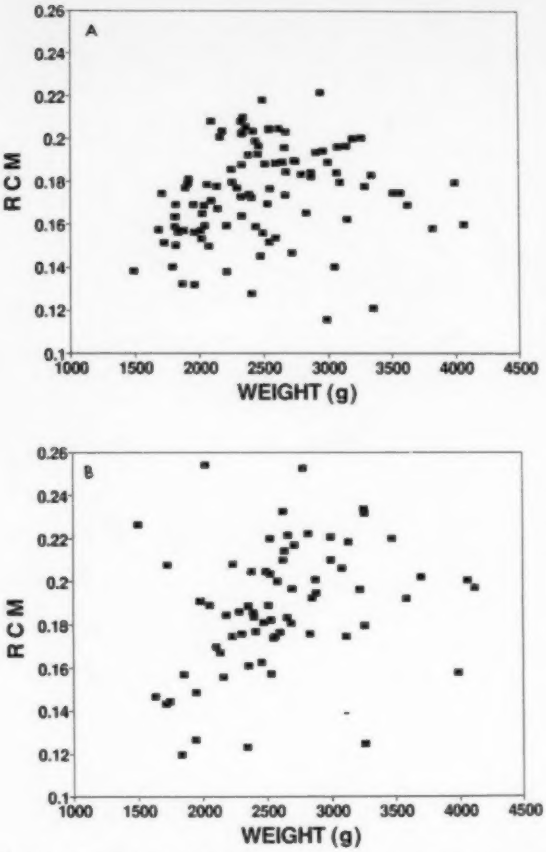

FIG. 10. Proportion of body weight allocated to ovaries (RCM) for Lake Erie walleye sampled in the spring of (A) 1991 and (B) 1992.

Fecundity of Walleye

Fecundity differed little with length (age) both between years and within years. Fecundity (log-linear (naperian)) was significantly correlated with forklength (millimetres) in both the autumn and spring (autumn 1990: $F = 0.0073L + 7.8068$, df = 125, $R^2 = 0.57$, $P < 0.0001$; autumn 1991: $F = 0.0065L + 8.5585$, df = 99, $R^2 = 0.74$, $P < 0.0001$); spring 1991: $F = 0.0050L + 9.1596$, df = 99, $R^2 = 0.39$, $P < 0.0001$; spring 1992: $F = 0.005L + 9.1233$, df = 68, $R^2 = 0.65$, $P < 0.0001$). From the autumn to the following spring, there was a small but significant increase in average fecundity (ANOVA, $P < 0.001$) from 1990 to 1991, but an insignificant decrease ($P = 0.54$) from 1991 to 1992. The ratio of lipids to protein in the eggs of Lake Erie walleye for 1991 and 1992 was similar and was unrelated to fecundity (spring 1991: ratio = 0.62 ± 0 .063 (SE); spring 1992: ratio = 0.63 ± 0.050 (SE)). Age was not a significant factor explaining the variability of fecundity (Type III ANOVA: $P(\text{age}) = 0.7317$, $P(\text{length}) = 0.0001$, ($P(\text{age·length}) = 0.8735$).

Fecundity was more appropriately related physiologically to body weight or ovarian weight. There were no great differences in the relationship between fecundity and round weight of walleye from Lake Erie and the Thames River (Fig. 9). Fecundity increased with ovary weight (fecundity =

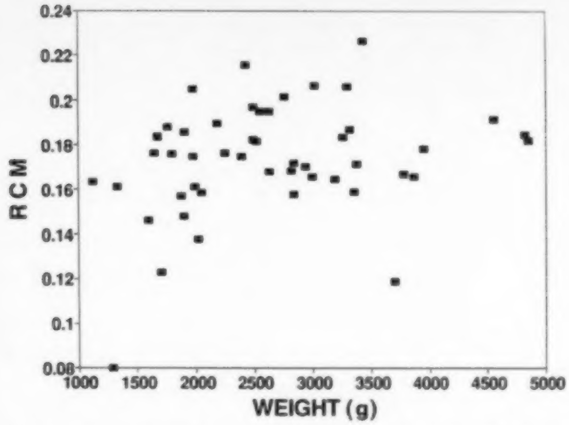

FIG. 11. Proportion of body weight allocated to ovaries (RCM) for Thames River walleye sampled in the spring of 1992.

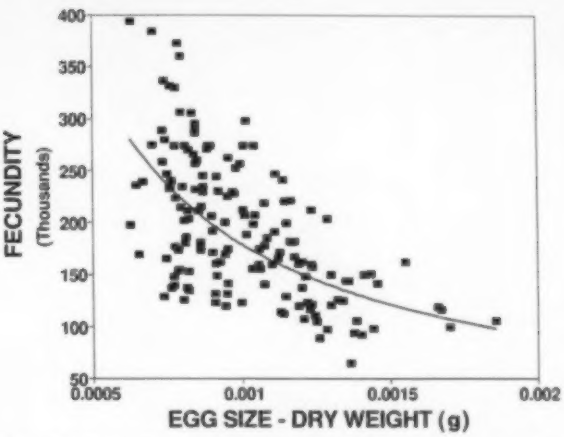

FIG. 12. Fecundity in relation to egg size (dry weight) of pooled walleye sample (springs of 1991 and 1992) from Lake Erie.

b·ovary weight, zero intercept model; autumn 1990: $F = 733.86\text{ovary}$, df = 99, $R^2 = 0.90$, $P < 0.0001$; spring 1991: $F = 383.66\text{ovary}$, df = 99, $R^2 = 0.97$, $P < 0.0001$; autumn 1991: $F = 759.69\text{ovary}$, df = 99, $R^2 = 0.98$, $P < 0.0001$; spring 1992: $F = 419.79\text{ovary}$, df = 68, $R^2 = 0.82$, $P < 0.000$). The proportion of total body weight allocated at spawning to ovaries (RCM) differed little between years or weight-classes of females; ovaries made up 12–25% of body weight (Fig. 10). The RCM of walleye spawning in the Thames River was also 12–23%, but varied less (Fig. 11). Since RCM could be considered constant or unrelated to body weight, one could infer that fecundity was related to body weight in a less variable way than to length. The regression of fecundity on forklength ($r = 0.62$ spring 1991, $r = 0.81$ spring 1992) was more variable than the regression on ovarian weight ($r = 0.98$ spring 1991, $r = 0.91$ spring 1992), which is in turn linearly related to body weight.

Egg size was inversely related to fecundity and, by implication, to body size and age as well. Fecundity (X) was inversely related to egg size (ES = grams per egg) in the spring (spring 1991: $\ln(F) = 5.815 - 0.906 \ln(\text{ES})$, df = 99, $R^2 = 0.33$, $P < 0.01$; spring 1992: $\ln(F) = 8.898 - 0.482 \ln(\text{ES})$, df = 57, $R^2 = 0.036$, $P < 0.01$; pooled regression: $\ln(F) = 5.438 - 0.96 \ln(\text{ES})$, df = 157, $r^2 = 0.40$) (Fig. 12). In the early autumn, there was a poorer inverse relation between fecundity and egg size (autumn 1990: df = 125, $R^2 = 0.11$, $P > 0.0001$; autumn 1991: df = 99, $R^2 = 0.10$, $P < 0.001$).

RCM was predominately in the range from 16 to 22%, but was uncorrelated with body weight in our samples from Lake Erie (Fig. 10). A similar range of RCMs was found amongst female from the Thames River (Fig. 11). Using the data provided by Pugsley (1983), we calculated that the RCMs of Talbot River walleye also fell within the same range. As with other body organs (Weatherley and Gill 1983), it appears that the RCM may vary little. Provided that the parameters of the relation between fecundity and egg size did not change between years and locations, we would not expect that fecundity would differ significantly between years and locations for females of a similar weight. Our estimates of fecundity did not differ substantially between 1991 and 1992. Baccante and Reid (1988) claimed that fecundity of walleye increased as population size decreased, as a function of the increased availability of food. McFadden et al. (1965), MacKay and Mann (1969), and Martin (1970) have also suggested that fecundity in freshwater fish was a function of the productivity of the water, but the evidence is insubstantial because of small sample sizes, lack of statistical significance, or methodological difficulties. In all of these studies, fecundity was correlated with length, but we feel that a more appropriate physiological correlation should be made with weight. Fecundity will increase in a length-class, only if the weight has increased.

We propose that because RCM is an allometric relation (Weatherley and Gill 1983), fecundity is a function of weight and will not differ significantly between years or locations, unless there was a substantial change in egg size. Thus, a complete ovary is one that meets, within some tolerable limits, the criterion of an RCM of about 18%; if this criterion is not met, then the female may not spawn. Variability is the one major difference between the RCMs of walleye caught in Lake Erie and the Thames River (Fig. 10 and 11); RCMs were more variable for Lake Erie than Thames River females. We were more confident that walleye ascending the Thames River were going to spawn; in contrast, walleye caught in Lake Erie were not caught on the spawning shoals. It is possible that walleye from the Lake Erie sample with RCMs below some level (16%) would not spawn. We are not sure what these deficient females do, but each year, a few females are caught after the spawning season with seemingly ripe ovaries.

We have also shown that the RCM expressed as a ratio of ovarian to total stored energy was inversely related to body size. Thus, larger females allocated a progressively smaller proportion of their available energy to reproduction. Furthermore, the lipid-RCM of spawners in the spring was smaller than the predicted ratios of the potential spawners sampled in the previous autumn. We interpret this to mean that not all of the apparently mature females sampled in the autumn actually spawn in the spring. This interpretation was corroborated by the observations that the actual spawners (spring) were larger and older than the apparent spawners assessed in the autumn.

Chemical Composition of Autumn and Spring Walleye

There was a significant decrease in the percentage dry weight of lipids in the whole carcass (somatic and gonadal

TABLE 1. Chemical composition of walleye collected in the western basin of Lake Erie from the autumn of 1990 to the spring of 1992. Somatic constituents estimated in the autumn included the undeveloped ovaries. Protein and lipids are expressed as percentage of dry weight (numbers in parentheses are standard errors).

Variable	Autumn 1990	Spring 1991	Autumn 1991	Spring 1992
Sample size	68	94	100	70
% somatic protein	56.4 (4.36)	56.1 (4.43)	na	52.6 (4.71)
% somatic lipid	30.6 (4.58)	25.3 (4.16)	23.5 (3.24)	27.8 (4.93)
% dry weight carcass	32.3 (2.06)	30.1 (2.52)	29.8 (2.06)	30.5 (2.31)
% wet lipid in carcass	10.1 (1.81)	7.7 (1.59)	7.0 (1.13)	8.5 (2.00)
Lipid energy per gram wet carcass weight	0.95 (0.171)	0.72 (0.151)	0.66 (0.107)	0.81 (0.189)
RCM-lipid (predicted)	0.29 (0.098)		0.33 (0.079)	
% ovary protein		55.3 (2.70)		52.0 (1.79)
% ovary lipid		34.1 (2.65)		32.7 (1.91)
% dry weight ovary		41.8 (2.37)		38.6 (3.22)
% wet lipid in ovary		14.3 (1.45)		12.6 (1.18)
Lipid energy per gram wet ovary weight		1.34 (0.137)		1.19 (0.111)
Ratio of lipid to protein in ovary		0.62 (0.063)		0.63 (0.050)
RCM-lipid (actual)		0.29 (0.058)		0.26 (0.061)

tissue) between the autumns of 1990 (30.6%) and 1991 (23.5%) (Table 1) before the gonads had fully developed. This decrease in lipid levels between the autumns of 1990 and 1991 largely explained the deficiency of surplus energy shown in Fig. 7. In the following springs, the percentage dry weights of lipids in the ovaries differed little (1991 lipid = 34.1%; 1992 lipid = 32.7%); however, the energy content (kilocalories of lipids per gram of spring ovaries) of the ovary in 1991 (1.39 kcal/g) was 13% higher than in 1992 (1.19 kcal/g) (Table 1). In comparison, the percentage dry weight of lipids in the spring carcasses (percentage somatic lipid) was higher in 1992 (lipid = 27.8%) than in 1991 (lipid = 25.3%). Spring protein composition was lower from both carcasses and ovaries in 1992 (carcass protein = 52.6%; ovary protein = 52.0%) than in 1991 (carcass protein = 56.1%; ovary protein = 55.3%). Notwithstanding these annual differences in protein and lipid composition, the ratios of lipids to proteins in the ovaries were similar (1991 = 0.62; 1992 = 0.63). Dry weights of the carcasses differed little between the springs of 1991 (30.1%) and 1992 (30.5%), but the dry weights of the ovaries (dry ovary weight/wet ovary weight) did decrease from 1991 (41.8%) to 1992 (38.6%). Overall, the 1992 spawners were in poorer condition in the preceding autumn (lipids) than the 1991 spawners. However, the composition of the ovaries differed less than somatic tissue. Thus, if a female produced an ovary, it was of good quality. The overall energy balance determined whether or not an ovary was produced at all.

Discussion

There were five main conclusions from our study. Maturation was dependent upon surplus energy sufficient for both metabolism and reproduction; this surplus was more likely available for larger and older walleye. Good year-classes are possible if most females have sufficient surplus energy. Not all females can replenish energy exhausted by reproduction and then have enough energy to spawn next year, thus partly explaining the dearth of strong consecutive year-classes. The early maturation of males was associated with a higher mortality, accelerated at the onset of maturation. Fecundity was inversely related to egg size, consistent with the idea that young fish behaved like semelparous and older fish like iteroparous spawners. All of these observations have implications for the management of walleye.

We propose that surplus energy is needed to provide an energy reserve for a period before, during, and after spawning; the consequences of not having enough surplus energy could be that spawning is foregone, growth is retarded, or natural mortality increases. Adult walleye show little growth until late summer (Colby et al. 1979). This retarded growth may reflect temporal changes in thermal conditions and abundance of suitable prey, as well as the consequence of compensating for a deficit of energy used in reproduction. Walleye probably do not feed much during the early cold part of the year. Thus, the elaboration of gonadal tissue is dependent upon successful foraging during the late summer and early autumn. We have no definitive way to demonstrate that there is a cost of reproduction for female walleye that use most of their surplus energy for reproduction. In evolutionary terms, early maturation may have been selected against if natural mortality was increased significantly as a consequence. If natural mortality increases with the proportion of stored energy allocated to reproduction (Shine and Schwarzkoff 1992) and not growth, the optimum age for reproduction (peak life time reproductive value (Fisher 1958)) is much greater than the observed first age at reproduction (Shine and Schwarzkoff 1992). This notion of cost (mortality) does provide a useful explanation for our observations. On average, only females with energy surplus to the requirements of reproduction contribute to the spawning stock. As a consequence, the spawners in Lake Erie were usually older than 4 yr or weighed more than 1800 g. However, even some of these older and larger females without sufficient surplus energy might not spawn, thus increasing their chances of surviving to spawn again. If we could monitor these individual females, we would be able to assess the cost of reproducing in relation to the individuals' energy reserves (Clutton-Brock et al. 1982).

Recruitment from the 1991 spawning was the best since 1986, but the 1992 year-class was weak (Fig. 1); the females that spawned in 1992 were in poor condition as evidenced by less and more variable surplus energy (Fig. 8). These 1992 spawners may not have recovered energetically from the previous year's spawning. Environmental conditions during incubation and feeding success after hatching could influence survival of young-of-year, and therefore affect year-class strength (Busch et al. 1975). Thus, the cost of reproduction (Reznick 1985) could explain why only those females that have energy in excess of the requirements for ovaries and metabolism before spawning can spawn. The proportion of females that spawn in any year is dependent upon the energetic condition of the stock at the end of the previous year's growth period.

Walleye recruitment is usually relatively poor following a strong year-class (Parsons 1970). We have no direct evidence that walleye do not spawn in consecutive years as shown for other species (Lambert and Dodson 1990), but walleye rarely produce consecutive strong year-classes even if the consecutive parental stocks were large (Henderson and Wong 1991). Intraspecific cannibalism may be one explanation for weak year-classes following strong ones (Henderson and Nepszy 1989); however, there is no evidence of cannibalism for walleye in Lake Erie (Knight et al. 1984). Another explanation is that spawning females experience an energy deficit after a strong year-class and are not able to accumulate enough surplus energy during the growing season following spawning to allocate sufficient energy for the next year's ovaries. Perhaps, strong year-classes are produced when all of the potential female spawners contribute eggs whereas weaker year-classes are produced when a smaller fraction of the females spawn.

Although we have no direct evidence for a cost of reproduction in terms of natural mortality to female walleye, we do have some evidence for a cost to males. Males, in contrast with females, allocate little energy to gonadal tissue, but in the case of salmonids, there is some evidence that male spawning behaviour requires significantly more energy than the female's behaviour and culminates in a higher mortality during the spawning period (Jonsson et al. 1991). Male walleye do spend more time on the spawning shoals (Eschmeyer 1950) and therefore probably do use more somatic energy than females during spawning. From the walleye population at large, the ratio of males to females declines with age (Fig. 4), particularly at the age of first maturation, implying that spawning males experience a higher mortality rate than females. The higher mortality of males may be a consequence of reproductive behaviour. The cost of reproduction by males and females may be expressed in different ways; the males may experience higher mortality rates whereas the females may have a reduced reproductive value by foregoing spawning in consecutive years. Further, longer-lived mature females will have a greater chance of reproducing than short-lived females in an environment with variations in weather during spawning and annual fluctuations of prey abundance in the growing season.

Curves of reproductive values for fish are different from other animals (birds: Woolfenden and Fitzpatrick 1984; mammals: Clutton-Brock et al. 1982) because fish in general continue growing after first maturation and fecundity increases with body size. In contrast with what is assumed for most fish, reproductive values of walleye increase to a peak at some age and then decline, assuming that the value of offspring or eggs is constant over all ages and adult mortality is a function of reproductive investment. The delay in reproduction that we have observed in walleye may be a consequence of the cost of premature maturation mediated through a reduction in growth and subsequent reduction in the residual reproductive value (Shine and Schwarzkoff 1992). However, Shine and Schwarzkoff (1992) did suggest that the cost of earlier maturation may be more affected by reduced survival than retarded growth. For males, we do have demographic evidence that survival declines after maturation. For females, the observation that egg size decreased as body size and fecundity increased (Fig. 12) can be interpreted as evidence for the effect of early maturation on subsequent survival. Fleming and Gross (1990) explained the positive relation between egg size and body size of coho salmon (*Oncorhynchus kisutch*) as the response of a semelparous breeder without any residual reproductive value. Thus, these semelparous breeders divert all of their surplus energy into larger gametes. Surplus energy increases as a power function of body size (Shuter and Post 1990), so larger fish would have larger eggs. In contrast, an iteroparous breeder (walleye) would not direct all of its surplus energy into gametes and therefore compromise its subsequent growth, survival, and residual reproductive value. Walleye fecundity and body size are inversely related to egg size. Smaller walleye will divert more of their surplus into each gamete if their survival rate declines more than large females as a function of spawning. Thus, there may be a dual strategy: upon first maturation, females either allocate all of their surplus energy into large eggs, if conditions are good, and then run the risk of death after spawning or, if conditions are poor, resorb eggs, postpone spawning, and opt for repetitive spawning but with smaller eggs in subsequent years.

The implications of these life history phenomena are relevant to the problems of fisheries management (Ware 1980). There are two main questions about the management of the walleye population in Lake Erie; what is the size of the population from which quotas are derived and how are catch quotas determined when population size declines?

The answer to the first question depends ultimately upon our estimate of natural mortality because this parameter strongly affects our estimate of population size from the Cagean model (Deriso et al. 1985); estimated population size is proportional to natural mortality. If, as we contend, natural mortality of males and females is significantly different, then the estimate of natural mortality used in the population model must be weighted by the proportion of males and females in the population. Alternatively, one should estimate separately the population sizes of males and females. At present, the estimate of natural mortality is partly dependent upon recaptures of individually marked walleye captured during the spawning period. Most of the tagged fish are young males, and therefore, the estimate of mortality is inflated because males experience a higher natural mortality. Thus, one could derive inflated estimates of abundance, and therefore, harvest more than one should. The estimate of natural mortality needs to be reviewed in light of these findings.

The second question could be answered if one knew either if a classical stock and recruitment relation existed (Ricker 1958) or what minimum stock size was needed to ensure the continued survival of the stock and the fishery if recruitment was unrelated to stock size and unpredictable. This study does not provide an answer to the second question, but it does help to define the spawning stock and describe the attributes of a spawning stock that will decrease the risk of extinction of profitable fisheries. First, we have shown that the spawning stock of females may be much smaller in number and older than previously thought. Second, the minimum stock size that would ensure the continued production of walleye must be based on the numbers of older mature females. Third, the potential recruitment from a spawning stock may depend upon the condition of the females. Ultimately, the allocation of surplus energy to growth, metabolism, and reproduction in reaction to body size may determine which females will spawn. Thus, larger females were more likely to spawn. Proximately, the condition of these potential spawners may also determine what proportion of the female spawning stock actually spawns depending upon their annual surplus energy. This surplus will depend upon the abundance and species composition of their prey, the initial condition of females after spawning, and the thermal conditions that limit the growing season. Therefore, both the age at first spawning and the incidence of consecutive spawning can be influenced by the annual condition of females.

Acknowledgments

The conceptual and practical contributions to this study by Jonathan Wong are much appreciated. Dr. Young Cho performed the chemical analyses for part of the samples. The field and technical staff at the Lake Erie Fisheries Station collected samples and did the preliminary measurements. In particular, we thank Allan Matthews for his help in coordinating the collections from the lake.

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Mixed-Species Yield-per-Recruit Simulations of the Effect of Seasonal Closure on a Central Queensland Coastal Prawn Trawling Ground

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Gribble, N., and M. Dredge. 1994. Mixed-species yield-per-recruit simulations of the effect of seasonal closure on a central Queensland coast prawn trawling ground. Can. J. Fish. Aquat. Sci. 51: 998–1011.

An assessment of the effect of seasonal closure on the central Queensland coastal prawn trawling grounds was carried out by mixed-species yield-per-recruit simulations of the fishery based on parameters determined from field studies and analysis of logbook data. Under a conventional scenario of constant fishing mortality, simulations suggest little positive effect on yield to be achieved from closures of up to 15 wk in duration. Economic gain would have to be made via reduced costs during the closure, rather than through increased value of the postclosure yield. Logbook data clearly showed that the fishery underwent a heavy pulse of effort, immediately after the fishing season opened. Nonlocal boats had entered the fishery to take advantage of the prawns available. Using this more realistic regime of fishing mortality, simulations suggest a significant increase in yield and value of catch. The increase was caused by boosted exploitation rates of the stocks and was determined by the magnitude of the effort pulse rather than as a direct benefit of the closure.

L'effet d'une fermeture saisonnière des terrains de pêche à la crevette sur le rendement par recrue pour une pêcherie poly-spécifique fut simulé utilisant des données obtenues par des études sur le terrain et l'analyse de carnets de pêche. En simulant des conditions conventionnelles de mortalité constante due à la pêche, le rendement ne serait que faiblement amélioré pour des fermetures durant jusqu'à 15 sem. Une réduction des coûts durant la fermeture plutôt qu'une augmentation de la valeur de la pêche après la fermeture devrait alors être à l'origine d'un gain économique. L'analyse des carnets de pêche fait clairement apparaître un accroissement temporaire de l'effort de pêche sitôt la saison de pêche ouverte. L'apparition de bateaux non locaux dans la pêcherie profitant des crevettes disponibles fut également notée. En simulant ces conditions plus réalistes de mortalité due à la pêche, on obtient une augmentation significative du rendement et de la valeur de la pêche. L'augmentation serait due à un taux d'exploitation des stocks plus élevé et serait liée à l'élévation temporaire du taux d'exploitation plutôt qu'à un bénéfice directement dû à la fermeture.

Received February 23, 1993
Accepted November 23, 1993
(JB816)

Reçu le 23 février 1993
Accepté le 23 novembre 1993

The objectives of fisheries management fall into three groups: maintenance or restoration of the resource, elimination or reduction of conflicts, and improvement of the economic performance of the fishery (Gulland 1988). Seasonal and spatial closures have been widely used as a means of maximising economic performance and/or production from prawn (cf. shrimp) fisheries in Australia, the Arabian Gulf, and the United States (Lucas et al. 1979; Somers 1985, 1990; Garcia 1989; Klima 1989). Identification and restriction of growth overfishing by seasonal closures are readily achieved in monospecific prawn fisheries which exhibit clearly defined recruitment events (Garcia 1989), at least in theory. When fisheries are based on more than one species and recruitment takes place over an extended period, management difficulties arise (Cobb and Caddy 1989). Prolonged availability to the fishery of a mix of young and older prawns means that maximising yield from each species may not be possible.

Seasonal closures on Queensland prawn grounds have been used as a yield-maximising technique since 1986 (J. Glaister, Queensland Department of Primary Industry, P.O. Box 46, Brisbane, personal communication), primarily to limit growth overfishing on brown prawns, *Penaeus esculentus*. The timing and effectiveness of the closures have been largely based on hearsay information from fishermen, with the exception of localised sampling in the Princess Charlotte Bay (15°S) area (Coles et al. 1985). Given the geographic range over which closures existed (11°S to 21°S), there was an obvious need to assess their applicability to regional fisheries. Two studies were initiated on coastal mixed-prawn fisheries by the Queensland Fish Management Authority, one centred on the Princess Charlotte Bay and the other between Bowen and Mackay (19°30′S and 21°30′S). In this paper the effectiveness of a seasonal closure of the

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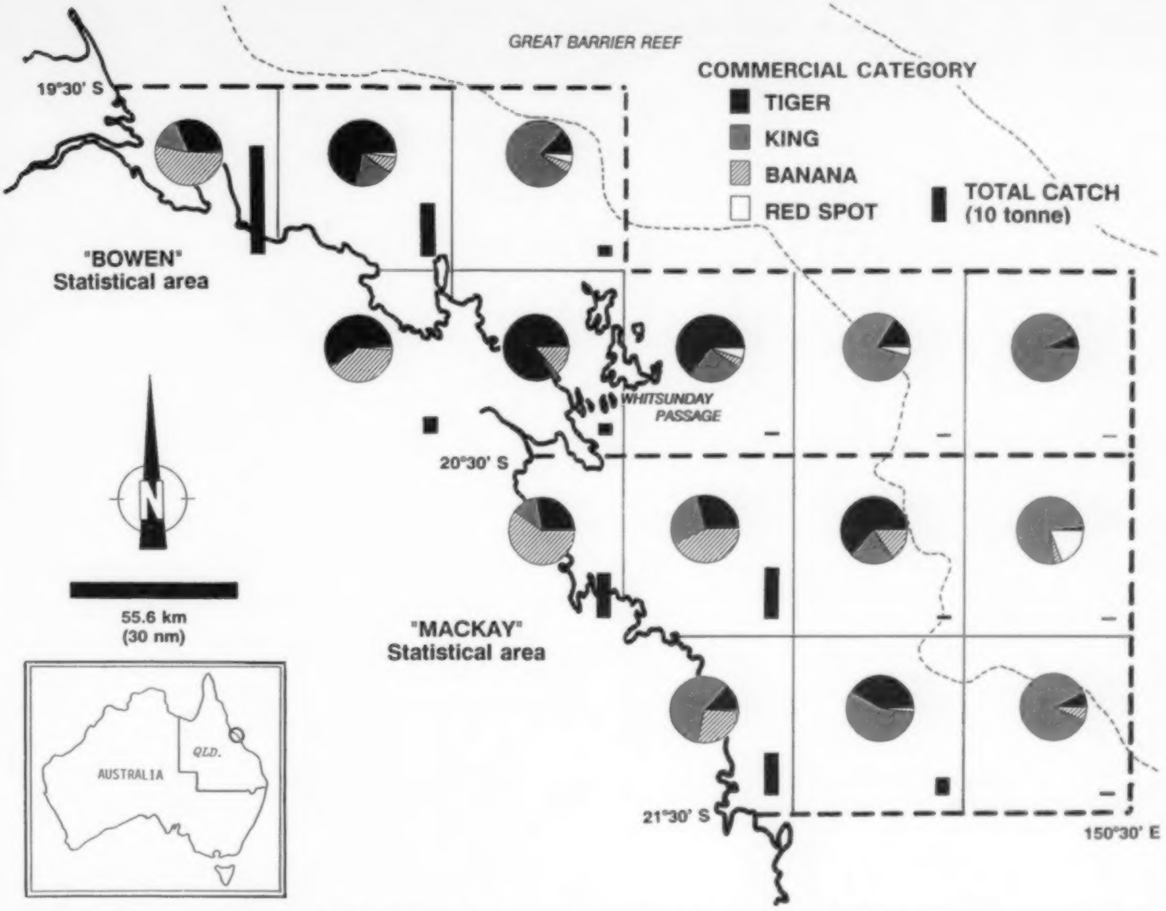

FIG. 1. Central Queensland coastal region between Bowen and Mackay (20°S, 147°30′E and 21°30′S, 150°30′E), overlayed with the CFISH logbook grid showing the Bowen and Mackay statistical areas (see text). Logbook data were entered as the common name category and not separated into species. The distribution of total prawn catch and catch composition by common name are shown as a bar and pie chart, respectively, in each grid.

coastal prawn trawling grounds in the Bowen/ Mackay region is evaluated.

Multispecies Yield-per-Recruit

Assessment of the seasonal closure was confined to the multiple single-species response approach (Sainsbury 1988) where each species was assumed to react to fishing pressure independently, with different responses being caused by different population parameters and fishing mortalities. Size-structured analogues of the Thompson–Bell yield-per-recruit model were developed for a multispecies assemblage, following Murawski (1984) and Pikitch (1987). The assemblage was exploited by an otter trawl fishery which was subject to a seasonal closure. This model was used to explore the consequences of multiple and/or prolonged recruitment, the effect of the duration of closure, and the effect of a pulse of fishing effort that had been observed immediately postclosure. Both yield-per-recruit (catch in kilograms) and utility-per-recruit (dollar value per commercial size category) implementations of the model were simulated.

The basic approach of the simulations was similar to that of Murawski (1984) and Pikitch (1987) in that technological interactions were considered rather than trophic or ecological interactions. An underlying assumption is that the component species in the mixed-species fishery exhibit mutually exclusive food resource partitioning and that interspecific competition for food is low. Morphologically similar prawn species co-occurring in the same area may exhibit some degree of resource competition; however, the intense trawling effort and resultant high fishing mortality that is applied to prawns are assumed to be the dominant effect on yield-per-recruit. Predation is taken into account via a coarse sensitivity analysis to varying natural mortality, but it is acknowledged that more complex interactions may exist between target species and bycatch that are competitors or predators (e.g., Brander and Bennett 1989).

One of the advantages of extending single-species yield-per-recruit models into a multispecies approach is the recognition that the mixed-species fishery may be the fundamental management unit, rather than any of its component species (Murawski 1984).

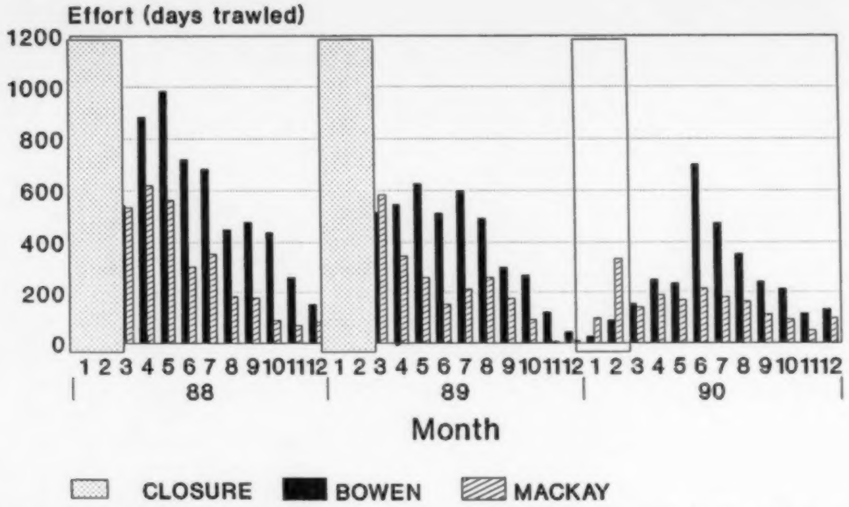

FIG. 2. Fishing effort for 1988–90 from the Bowen and Mackay statistical areas taken from the Queensland Fisheries Management Authority CFISH logbook database.

Description of the Fishery

Prawn fisheries off the Queensland coast, inshore of the Great Barrier Reef from latitude 12°S to 21°S, are based on at least six species of *Penaeus* and four species of *Metapenaeus*. Two species of *Trachypenaeus* and three species of *Parapaeneopsis* are also taken as marketable bycatch. In Bowen/Mackay the regional fishery is based on export grade tiger prawns, *Penaeus esculentus* and *Penaeus semisulcatus*, blue leg king prawns, *Penaeus latisulcatus*, and banana prawns, *Pernaeus merguiensis*, with a minor component being the endeavour prawns, *Metapenaeus endeavouri* and *Metapenaeus ensis*, which are sold locally. The coastal tiger prawn fishery is the most valuable of these in dollar terms (Trainor 1990).

The Queensland east coast otter trawl prawn fleet is "limited" entry with 868 boats licensed to trawl along 1200 nautical miles (2220 km) of coast (Trainor 1990). The Bowen/Mackay region, as part of this east coast fishery, could conceivably have up to the maximum of 868 boats fishing legally along the 150 km of its coast.

Parameter Estimation

Parameter estimates for the model were derived from four major data collection subprojects carried out on the central Queensland coast between 1988 and 1990 (Gribble and Dredge 1991, 1992): (1) research trawls using twin 6.6-m beam trawls at 2-wk intervals (lunar) at two sites within the Bowen and Mackay statistical areas (Fig. 1), throughout the 1989 seasonal closure and over the same period in 1990, when no closure was in force, (2) tag and release of prawns during the 1989 closure and during the same period in 1990, with subsequent recapture by the fishing fleet, (3) purchase of 3-kg samples of commercial catch and on-board monitoring of catch with participating local skippers, and (4) fine-scale, shot-by-shot research logbooks completed by participating skippers, in conjunction with the compulsory Queensland Fish Management Authority logbook program, CFISH.

Catch Composition and Fishing Effort (Logbook Data)

For the purpose of summarising the logbook record data, two approximately equal "statistical" areas were extracted as subsets from the Queensland Fish Management Authority CFISH logbook database. The Whitsunday Passage formed a natural division between the Bowen and Mackay areas, as trawling was not permitted within the passage (Fig. 1). In both CFISH and the research logbook databases, prawns were recorded under their common names and neither tiger nor endeavour prawns were separated into their component species. The fine-scale research logbooks showed that trawlers fished in both Bowen and Mackay for approximately equal times throughout the year and their catch was a composite of species available in each area.

Tigers and bananas were the predominant commercial category of prawns caught from Bowen, while approximately equal proportions of tigers, bananas, and king prawns were caught from Mackay. The distribution of total catch and catch composition is summarised in Fig. 1. For the closure assessment, it was assumed that a typical boat would trawl both the Bowen and Mackay areas and engage in daytime banana trawling when these prawns were available.

At both Bowen and Mackay, a pulse of fishing effort occurred after the start of the fishing season in 1988 and 1989 (see Fig. 2). A seasonal closure was not enforced in 1989–90 with the result that no pulse of effort occurred in March 1990 as had occurred in the previous two years. A more even pattern of effort was recorded with a maximum occurring around June–July 1990. The summed yearly effort recorded from Bowen dropped 28% between 1989 and 1990, while a drop of 13% was recorded from Mackay.

For the purposes of the model the pulse of effort observed in 1988 and 1989 was simplified to a linear ramp function with the peak fishing mortality ($F_{(\mathrm{PEAK})}$) occurring at the start of the fishing season (weeks) and decreasing as the year progressed (see Appendix).

Species Composition (Research Trawls)

In both 1989 and 1990, tiger prawns (brown tiger, *P. esculentus*, plus grooved tiger, *P. semisulcatus*) made up at least

TABLE 1. Species composition and midyear "counts-per-pound" value of catch (A$·kg^{-1}) used in the simulations of the central Queensland coastal mixed-species prawn fishery. Counts-per-pound is a traditional capacity measure, e.g., "30+" means at least 30 small prawns per imperial pound (14·kg^{-1}) and "<10" means large prawns with no more than 10 individuals·imperial pound^{-1} (4.5·kg^{-1}).

Species	% composition (by weight)	Counts-per-pound			
		30+	20–30	20–10	<10
P. esculentus	25	4.00	10.00	13.20	16.20
P. semisulcatus	25	4.00	10.00	13.20	16.20
P. latisulcatus	15	3.00	6.00	9.50	—
P. merguiensis	35	3.00	3.00	5.50	—
M. endeavouri	1	4.00	5.00	7.00	—
M. ensis	1	4.00	5.00	7.00	—

50% of the total weight of prawns caught in each sampling area. At Mackay, over 94% by weight of the tiger prawns caught were *P. esculentus*, but at Bowen the ratio between tiger species was approximately 50:50. *Penaeus latisulcatus* made up the next largest proportion by weight of the catch at Mackay, but by comparison, very few blue leg king prawns were caught at Bowen. The total *P. latisulcatus* catch from both areas varied from 13 to 34% of the catch between 1989 and 1990.

Penaeus merguiensis, normally considered a daytime fishery, were caught at all sites even though trawling was carried out at night. Catches tended to be sporadic, but over the duration of the sampling in 1989, banana prawns made up a maximum 15% of the catch by weight. In 1990 the catch of banana prawns totalled a maximum of 10% of the catch by weight.

Metapenaeus endeavouri plus *M. ensis* were numerically important at each site, at approximately 25% of the catch. They were less important in terms of weight, dropping below 10–11% of the catch. This drop reflects the small size of the prawns caught. It was assumed that the absence of larger life history stages meant that these species matured outside the sampling areas.

The other species caught, *Metapenaeus bennettae*, *Penaeus japonicus*, *Penaeus monodon*, and *Penaeus longistylus*, were of minor importance in terms of number and weight.

In summary, research showed that the four commercial categories recorded in the logbooks were made up of at least six species, the composition of which varied both between sites spaced less than 90 nautical miles (150 km) apart and between successive years. The generalised species composition for Bowen/Mackay and midseason dollar value of commercial "count-per-pound" categories, shown in Table 1, were derived from the logbook records, research trawl data, and price data supplied by local processors and was based on a "typical" boat fishing in both areas.

Growth (Tag/Recapture and MPA Data)

von Bertalanffy's growth equation ($L_t = L_\infty\ (1 - \exp^{(-k(t-t_0))}]$) was fitted to the *P. esculentus*, *P. semisulcatus*, and *P. latisulcatus* tag return data using Fabens' (1965) nonlinear fit algorithm. Only data from prawns at large for 14 d or longer (see Hill and Wassenberg 1985) were included and outliers were identified and removed following initial fitting (see Table 2). Growth data on *P. merguiensis* were derived from modal progression analysis (Sparre et al. 1989) and a combination of MPA and limited tag return data (following Morgan 1987; Gayanilo et al. 1989). Growth parameters for *M. endeavouri* and *M. ensis* were taken from Buckworth (1989).

TABLE 2. von Bertalanffy growth parameters calculated from 1989 and 1990 prawn tag return data from coastal central Queensland (L_∞ is carapace length in mm).

Species	Sex	L_∞	*K*	*n*
1989				
P. esculentus	F	45.4	0.0556	54
	M	36.7	0.0536	92
P. semisulcatus	F	51.9	0.0408	51
	M	37.4	0.0723	56
P. merguiensis	F	40.5	0.1235	7 (1517)[a]
	M	33.6	0.1462	11 (2075)[a]
1990				
P. esculentus	F	46.3	0.0436	144
	M	37.8	0.0528	156
P. semisulcatus[b]	F	46.4	0.0363	74
	M	36.1	0.0615	112
P. latisulcatus	F	44.1	0.0690	46
	M	36.4	0.0990	36

[a] Number of prawns used for growth estimates from length frequency modal progression analysis and limited tag returns.

[b] Research trawl data in 1990 indicated that the average largest size of a female was 50.2 mm CL (n = 22 or 2.4%, max. = 53.8, min. = 48.2), suggesting the target population may not have been representative of the total population in this year.

Morphometric Parameters (Research Trawling)

Length–weight relationships were determined for each species and gender (Table 3). Carapace length (CL) is used as defined by Sparre et al. (1989).

Movement (Tag Data)

As tagged prawns could be recaptured at any point during a commercial trawl, the accuracy of the reported position of recapture was dependent on the trawl duration, i.e., approximately 2 h at 3 kn or 6 nautical miles (11 km) for this fishery. Movement of under 6 nautical miles could not be reliably distinguished from "no movement". In 1989, 66% of the recaptured tagged prawns of all species had moved less than 6 nautical miles, while 12% had moved

TABLE 3. Allometric relationship (wt = a CL^b) of prawn species from coastal central Queensland, where wt is in g and CL is in mm.

Species	Sex	a	b	n	r^2
P. esculentus	F	0.00211	2.7513	7080	0.99
	M	0.00164	2.8381	7024	0.98
P. semisulcatus	F	0.00180	2.7776	3362	0.99
	M	0.00149	2.8518	3334	0.99
P. latisulcatus	F	0.00100	2.8444	1002	0.98
	M	0.00077	2.9366	1019	0.97
P. merguiensis	F	0.00200	2.7392	2617	0.98
	M	0.00152	2.8364	2019	0.97
M. endeavouri[a]	F	0.00191	2.7470	862	0.99
	M	0.00160	2.8274	745	0.98
M. ensis[b]	F	0.00193	2.7623	4319	0.98
	M	0.00169	2.7188	4046	0.92

[a] Data from Torres Straits courtesy of QDPI Northern Fisheries.

[b] Data from central Queensland but may not be representative of the larger adults (see text).

greater than 12 nautical miles. In 1990, 73% of recaptured tagged prawns had moved less than 6 nautical miles and 6% had moved greater than 12 nautical miles.

Based on the tag/recapture data, two assumptions were made for the period of the fishing season simulated: the prawn populations were essentially local and emigration and immigration would have minor effects on population dynamics.

Natural Mortality (Tag Data)

Natural mortality was estimated from sequential tag releases according to Dredge (1990); however, the very high estimates based on the data collected in 1989 were considered biologically unrealistic. A major bias appeared to have been introduced by the nonreporting of tags caught by large trawlers passing through the fishery at the start of the fishing season. Even allowing for an estimated 30% nonreporting of tags from the first release, the values for natural mortality were 2–3 times higher than reported in the literature (Garcia and LeReste 1982; Garcia 1985).

Instantaneous total mortality was estimated (Ricker 1975) using tag returns from the two 1990 releases. A seasonal closure was not enforced in 1989–90 which meant that returns were not biased by nonreporting at the beginning of the season (Gribble and Dredge 1992); however, without the closure, natural mortality could not be calculated according to the method of Dredge (1990).

The wide variation in estimates of the rate of natural mortality indicated that simulations should allow different levels of natural mortality to be investigated. A range of M between 0.05 to 0.20·wk^{-1} was chosen, going from the accepted level of natural mortality in prawns (Garcia and LeReste 1982) to 4 times the accepted level.

Gear Selection Characteristics (Research Trawl)

A series of beam trawl trials comparing 19-, 38-, and 50-mm-mesh trawl nets were carried out in 1989 and 1990. Small prawns in large numbers were not available from all species at the same time; hence, there were gaps in the net selection data. Use was made of results from net selection trials using otter board gear previously carried out off Townsville (M. Dredge, unpublished data). To validate this procedure, a series of comparisons were run alternating beam trawls with otter boards pulling the same 38-mm-mesh nets. Otter board trawls caught greater numbers of prawns, but neither species composition nor size distribution of the catch was significantly different (Kolmogrov–Smirnov statistic at the $P < 0.05$ level).

TABLE 4. Net selection characteristics for prawn beam and otter trawl gear. L50%, L75%, and L100% are the CL in mm at which 50, 75, and 100% of prawns caught by the net are retained (Pope 1966).

Species	Net (mm)	L50%	L75%	L100%
P. esculentus and *P. semisulcatus*	38	15.7	16.3	17.4
	50	24.3	28.3	34.0
P. latisulcatus	38	—	—	—
	50	22.2	25.0	31.0
P. merguiensis	38	15.0	18.0	25.0
	50	15.5	18.0	26.5
M. ensis and *M. endeavouri*	38	13.4	14.8	18.1
	50	20.0	22.0	26.0

The fishery does not distinguish between tigers nor are the endeavour prawn species separated. Given the morphological similarity of the prawns, data on net selection of the two tiger prawn species were combined as were the data on the two endeavour prawns (see Table 4). Net selection parameters S, $S1$, and $S2$ were estimated according to Sparre et al. (1989).

Recruitment (Research Trawl and Commercial Samples)

A generalised scheme for the timing and strength of recruitment of the four major commercial prawn species (Fig. 3) was used for subsequent simulations. Endeavour prawns, *M. endeavouri* and *M. ensis*, were present throughout the sampling period as small prawns. For the purposes of the model, these species were taken as continuous (or multicohort) recruiters. The recruitment parameters of a total of six species were included in the simulations: the two species of tiger prawns, blue leg king prawns, banana prawns, and both species of endeavour prawns.

The model allowed recruits to be entered each week of a simulation; hence, a profile of a pulse of recruitment could be built up over a number of weeks. Multiple and continuous recruitment could be simulated in a corresponding fashion.

Simulations

Variations on the 1988–89 seasonal closure were simulated to give both yield (catch in kilograms) and utility (A$ value per commercial size category) estimates. Results are illustrated by response surfaces (Dillon 1968) showing the effect on relative yield or value of increasing pulse fishing mortality and duration of seasonal closure. Each response surface represents a matrix of two hundred and twenty-five 52-wk summations of simulated yield and/or value for various combinations of peak fishing mortality and closure duration.

Individual simulations were started in the equivalent of October–November, to include the summer recruitment peaks, and then stepped through 52 wk of fishing. It was assumed that the majority of prawns recruited would be caught in the first year, allowing the simulations to terminate before the

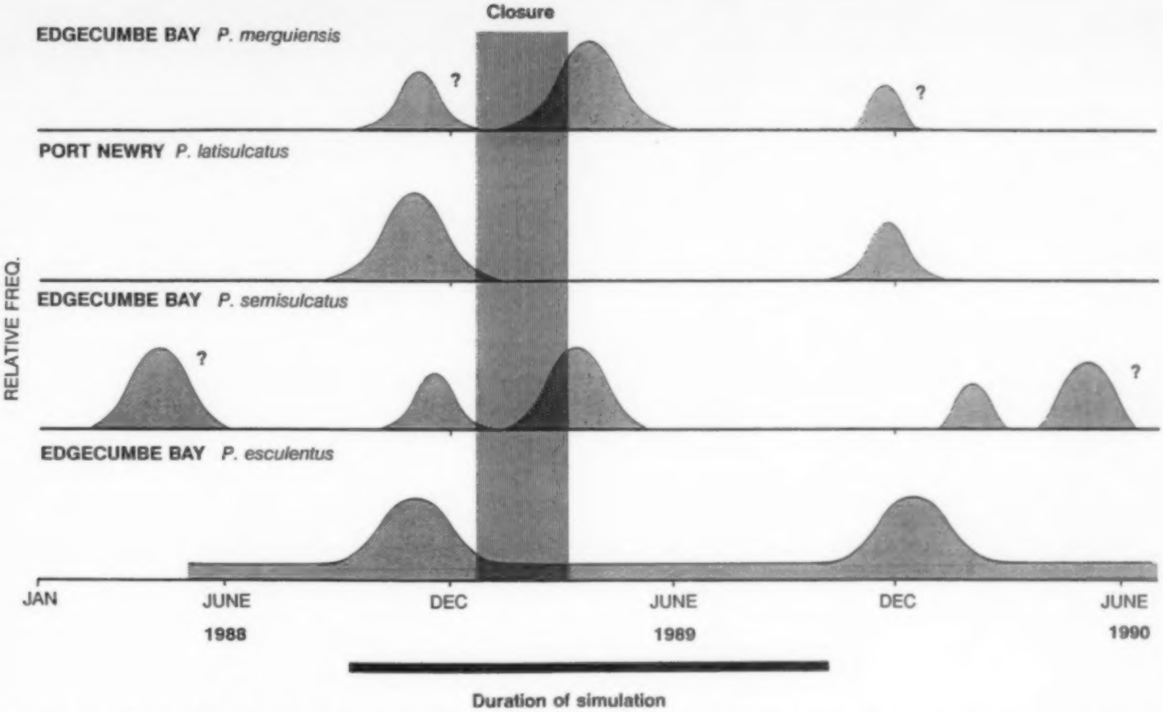

FIG. 3. Generalised scheme for the timing and strength of recruitment of prawns <20 mm CL for the four major commercial prawn species in the Bowen/Mackay region.

next year's seasonal closure began. For each week of a simulation, growth, mortality, catch weight, and catch value were calculated for both sexes of six commercial species of prawn. Summed yield and/or value were weighted by the percentage species composition of the simulated catch (following Murawski 1984). The number of recruits and the timing of recruitment of each species were held constant for all simulations; hence, output is presented as relative yield and value of the simulation rather than attributed to a recruit of a species or to a "composite" recruit of all species.

Simulations were not carried out using recruitment timing derived from the 1990 survey. The delay and reduced strength of the first recruitment peaks observed in 1990 meant that a closure similar to that of 1988–89 would have been too early and too short to have protected recruiting prawns from growth overfishing. Computer simulation was not required to prove what was obvious to local fishermen.

Simulation Scenarios and Results

The following scenarios were simulated and results summarised:

(1) Assuming no pulse of fishing effort occurs at the start of the season and a closure of variable duration starts in late December, i.e., variations on the 1988–89 closure under a conventional scenario of constant fishing mortality. The simulation indicated that (i) yield in kilograms drops for all closure durations compared with a zero duration closure (i.e., no seasonal closure) and (ii) value of yield (utility) increases marginally with increased closure duration. This increase is due primarily to the disproportionately higher price gained for the larger brown tiger prawns from the spring–summer recruitment.

(2) Assuming no pulse of effort occurs and a 6-wk closure starts in mid-February, i.e., protecting the autumn pulse of grooved tiger and blue leg king prawn recruits rather than the spring–summer recruits. Results show that both yield and value were lower than if no closure occurs.

(3) Given that a pulse of fishing effort (i.e., $F_{(PEAK)}$) occurs at the start of the season and diminishes with time indicates that (i) yield and value increase asymptotically over closure durations of from 3 to 15 wk and for peak fishing mortality equivalent to $F_{(PEAK)} = 0.06$ (normal fishing pressure) to $F_{(PEAK)} = 0.19$ (a pulse of approximately 4 times normal fishing pressure); (ii) for closure duration of from 3 to 9 wk, yield and value decrease below $F_{(PEAK)} = 0.06$, i.e., as for the no pulse of effort scenario (beyond 10 wk closure duration the yield continues to drop but value increases slightly (Fig. 4, 5a, and 5b)); (iii) holding the closure duration at 1 wk and increasing $F_{(PEAK)}$ from 0.05 to 0.19 decreased the percentage of 10–20 counts-per-pound in the catch while conversely increasing the percentage of smaller prawns caught (Fig. 5c and 5a); (iv) holding the $F_{(PEAK)}$ at 0.05 and increasing the closure duration from 1 to 15 wk increased the percentage of 10–20 counts-per-pound tiger prawns caught while decreasing the percentage of smaller prawns (the exception was in the endeavour prawn where the percentage of small prawns caught rose marginally (Fig. 5c and 5d)); and (v) increasing both the closure duration from 1 to 15 wk and $F_{(PEAK)}$ from 0.05 to 0.19 gave an increase in the percentage of both 10–20 and <10 counts-per-pound categories of all species caught (Fig. 5c and 5b).

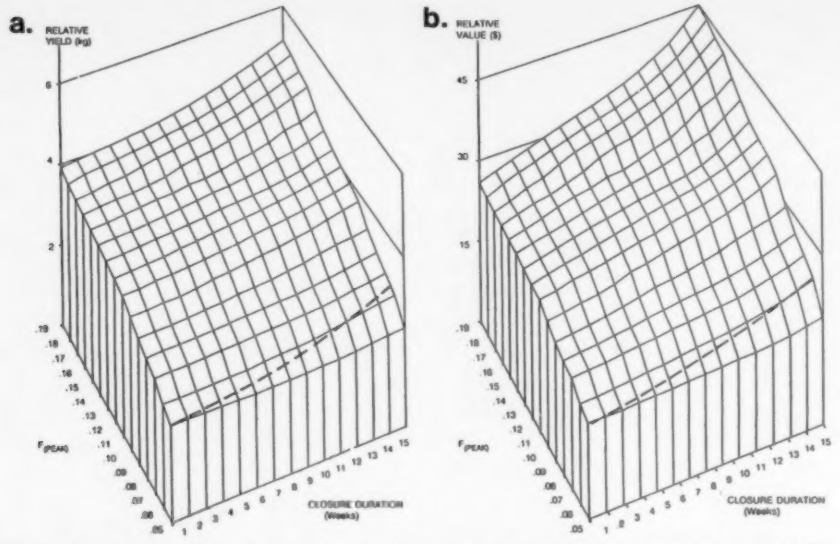

FIG. 4. Relative (a) yield and (b) value of yield (utility) simulated by the multispecies yield-per-recruit model (see text) of prawns from the Bowen/Mackay region, given that a "ramp" pulse of effort occurs following a seasonal closure. The broken ridge line illustrates results where the yearly effort was redistributed but not increased.

(4) Where the closure duration and $F_{(PEAK)}$ combination gave a total annual fishing mortality equal to the no closure scenario ($F = 2.26 \cdot yr^{-1}$), i.e., where the yearly effort was redistributed but not increased, yield and value increase; approximately 11 and 26% of the maximum values simulated at $F = 0.5 \cdot wk^{-1}$ with no closure (broken ridge lines on surface response plot, Fig. 4).

(5) For combinations of closure duration and $F_{(PEAK)}$ resulting in fishing mortality greater than $F = 2.6 \cdot wk^{-1}$, i.e., where effort was "created" not just redistributed. Simulations indicated that predicted yield and value rose dramatically (Fig. 4).

(6) Within a wide but realistic range of natural mortalities ($M = 0.05–0.20 \cdot wk^{-1}$) and within the range of peak fishing intensities and closure durations simulated in scenario 3 above, (i) increased values of M tended to flatten the value and yield response surfaces (see Appendix, Fig. A1) (a 50% decrease in maximum yield occurred when natural mortality was increased from 0.05 to $0.10 \cdot wk^{-1}$ with a concomitant 55% decrease in maximum value; at $M = 0.20 \cdot wk^{-1}$, maximum yield was down to 19% and maximum value was down to 14% of the values simulated at $M = 0.05 \cdot wk^{-1}$) and (ii) the value profile simulated at $F_{(PEAK)} = 0.05 \cdot wk^{-1}$ (normal fishing pressure) changed from a slight increase with increasing duration of the seasonal closure to a slight decrease.

Discussion

In a multispecies system, the relative recruitment strength between species is unlikely to remain constant between years (Murawski 1984; Garcia 1989). Whilst spawning and recruitment of penaeid prawns can usually be modelled on the basis of annual or biannual cycles (Garcia and LeReste 1982; Crocus 1987), there is little evidence that recruitment onto Australian trawling grounds is simultaneous in multiple-species fisheries or instantaneous in most single-species fisheries. Coles et al. (1985) described consecutive recruitment of the tiger prawns *P. esculentus* and *P. semisulcatus* in Princess Charlotte Bay, north Queensland, Somers and Kirkwood (1991) showed an extended recruitment period for *P. semisulcatus* in the Gulf of Carpentaria, and Penn et al. (1989) noted the latitudinal variation in timing and pattern of recruitment of both *P. esculentus* and *P. latisulcatus*. Furthermore, Garcia et al. (1984) and Garcia (1989) stressed that annual variation in recruitment of prawns (shrimp) occurs generally and can be induced by environmental conditions. Data presented in this paper also indicate that not only can individual prawn species have extended or multipulse recruitment, but also that different species move onto the fishing grounds at different times of the year.

Managing the fishery to achieve optimum yield-per-recruit or maximum yield becomes even more complex when interannual variation in the timing of recruitment is a factor, as was the case in the Bowen/Mackay region between 1989 and 1990. Our data, however, do show that recruitment largely occurs during a 4-mo period from midsummer to autumn, which is consistent with the findings of Lucas et al. (1979), Somers et al. (1987), Penn et al. (1989), and Somers and Kirkwood (1991) for subtropical prawn species in Australia.

Simulations based on the mixed-species yield-per-recruit and value-per-recruit models proposed in this paper, using input parameters derived from biological and economic data collected in 1989, indicate that in the absence of a pulse of fishing effort at the commencement of the fishing season, a relatively short closure starting in late December may benefit the fishery owing to (i) a small increase in the total yield value, largely brought about by the capture of larger (and more valuable) prawns, (ii) cost savings made through not fishing during the closure, and (iii) total fishing effort and fishing mortality being reduced, hence reducing pressure on the stock levels.

Should a pulse of effort occur, but total fishing mortality be equivalent to a no closure situation (i.e., the year's

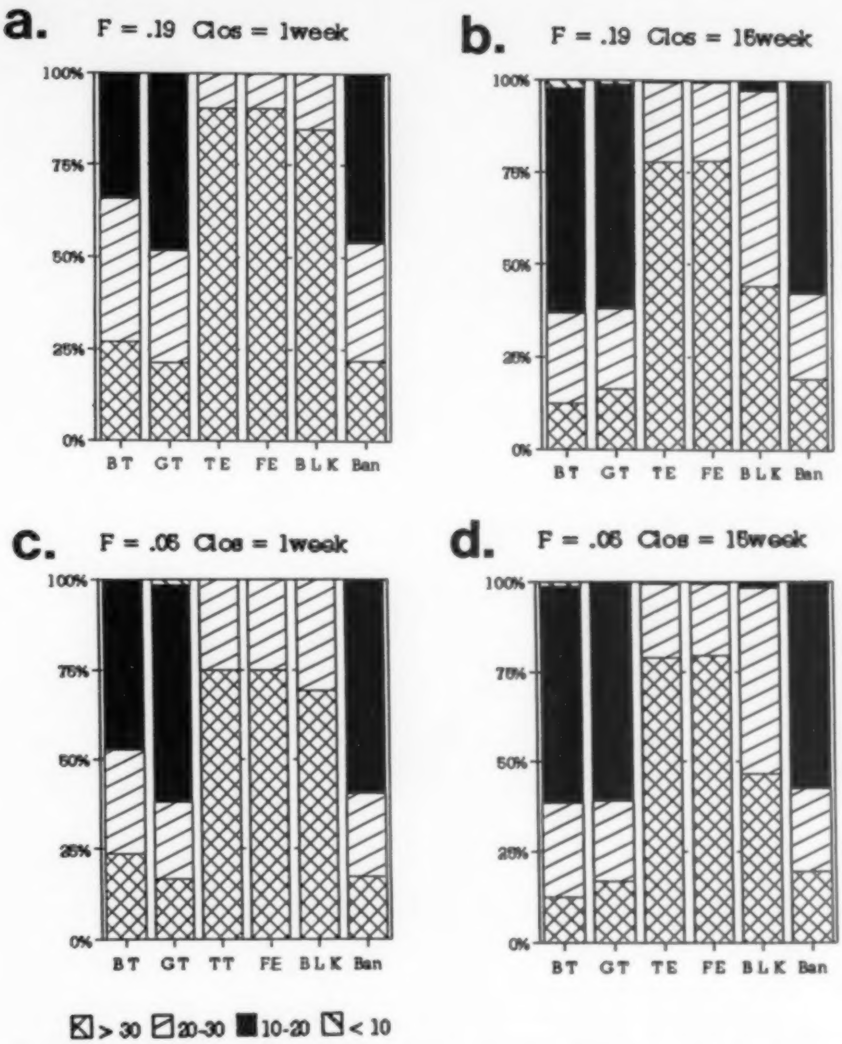

FIG. 5. Percentage by weight of commercial size categories (counts-per-pound) of the most economically important prawn species as simulated for the Bowen/Mackay region for increasing duration of closure and increasing magnitude of the fishing effort pulse. BT, brown tiger; GT, grooved tiger; TE, true endeavour; FE, false endeavour; BLK, blue leg king; Ban, banana.

effort is redistributed but not increased), then benefits to the fishery will be similar to the above, with the exception that stock levels will be under heavier pressure.

In the scenario of a closure followed by an effort pulse and subsequent fishing effort sufficient to increase total annual fishing mortality, total value of catch from the fishery will be increased. The increase is attributable both to increased exploitation and to a lesser degree to increased average size (and value) of prawns. Simulations indicate the increase in catch is proportional to the increase in effort, and presumably so are catch-costs, directed at the prawn stocks. This scenario can readily be associated with economic overfishing (Somers 1990) and may ultimately lead to stock/recruitment dysfunction (Penn et al. 1989).

Inspection of the 1989–90 logbook data revealed that the pulse in fishing intensity was not simply a redistribution of effort normally applied in the fishery, but was due to additional effort. In 1989, when a seasonal closure was applied to the study area, total fishing effort was some 25% more than in 1990, when there was no closure. Boats appear to have moved onto the grounds, and local boats applied greater effort, in order to take advantage of the availability of prawns at the beginning of the season. Thus, seasonal closures have the ability to institute social changes, in the sense of reallocating catch between "local" fleets and those "nonlocals" prepared to travel in the expectation of taking higher catches.

Yield and utility optimisation as applied in this assessment are contingent on a number of extrinsic variables. The influence of a price structure, heavily weighted in favour of large "export-grade" tiger prawns *P. esculentus* and *P. semisulcatus*, resulted in the model being extremely sensitive to both relative numbers and size of these species. As *P. esculentus* dominated the tiger prawn catch in the Mackay area, and this species had a single pulse of recruitment prior to the opening of the season, the utility from the tiger prawn component of the fishery was close to optimal. In the Bowen area, however, the presence of equal numbers of two tiger prawn species, one of which had a second pulse of recruits after the season opened, would have resulted in growth overfishing on part of the combined stock so giving suboptimum yield and utility.

Banana prawns *P. merguiensis* give another example of how price structure may influence multispecies utility models. Both research logbook and compulsory logbook data indicate that the abundance for the species was reasonably high in 1989. At the time, however, the price for *P. merguiensis* was low, both as a consequence of factors influencing international market prices (Smith et al. 1991) and because of an elastic demand curve on local markets. In this instance, market forces were more significant than population dynamics in determining the contribution made by banana prawns in optimising a mixed-species value and value-per-recruit estimate.

In the present study, estimates of yield and utility derived from simulations were also highly sensitive to variation in natural mortality. Although a natural mortality rate of $0.05 \cdot wk^{-1}$ has been frequently quoted for prawns (Lucas et al. 1979; Garcia and LeReste 1982; Glaister et al. 1990; Somers 1990), predation studies have shown that fish predators alone may account for a greater mortality rate (Pauly and Palomares 1987; Dall et al. 1990). Dredge (1990) estimated that instantaneous natural mortality for *P. longistylus* in the Townsville region (100 km north of Bowen) was $0.072 \cdot wk^{-1}$. Benefits from a seasonal closure in the Bowen/Mackay region would be markedly reduced should a similar natural mortality level apply to target species in that area.

Critical model parameters in addition to natural mortality were estimates of relative recruitment strength and timing and fishing effort (mortality). It was necessary to incorporate a number of simplifying assumptions in the model in relation to these parameters. Natural mortality was assumed to be constant across the size classes retained in the fishery. Dall et al. (1990) have given approximations of relative mortality for larvae, juveniles, subadults, and adults. No attempt has been made to include this level of complexity into the models, as the estimates of total natural mortality were imprecise to begin with. Rather, a stepped range of values was chosen to test the effect of coarse-scale variation in the parameter.

Recruitment was observed to vary in terms of both relative species abundance and on an interannual basis. Such variation could be expected to have a considerable impact on the effectiveness of a fixed closed season. To allow for interannual variation in recruitment, Garcia (1989) proposed a flexible closed season with the opening date based on preseason surveys, although he acknowledged that inefficiencies may arise in multispecies fisheries. An alternative measure is to use the risk-management concept of a fixed opening date which gives an acceptable approximation of an optimum yield for an "average" year. For example, a fixed seasonal closure that achieves 95% of optimum yield in 7 out of 10 years may be considered acceptable. For the Bowen/Mackay fishery, simulations were limited to the 1989 recruitment pattern and the general applicability of the results are dependent on how typical that year is of the long-term recruitment pattern.

Although the Queensland east coast prawn fishery is "limited" entry at 868 boats, movement of this fleet is not restricted (zoned) which means high concentrations of trawlers can occur in regional fisheries following seasonal closures. This situation is comparable with that in the Gulf of Mexico where 4999 boats were operating in 1985 (Klima 1989) and local closures (off Texas) attracted an unwanted concentration of vessels at the opening of the shrimp season. The resultant pulse fishing and increased effort at the beginning of the season were estimated to decrease the yield per individual fisherman, yet total value did not decrease until effort increased beyond 45% (Nicholas, as reported in Klima 1989). This is similar to results indicated from simulations of the Queensland central coast prawn fishery.

There is little advantage to be gained from regulating temporal fishing effort patterns by closures without also limiting fishing capacity; gains from optimising the size composition of the catch will be lost if fishing capacity is allowed to increase, but a limit on fleet fishing capacity alone will not ensure optimal size composition (Pauly 1979; Gulland 1988; Garcia 1989; Somers 1990). Garcia (1989) made the general statement that applies in this case: "the regulation of size at first capture (by seasonal closures) is likely to be inefficient if the total effort level is not properly controlled and perfectly in line with optimisation theory."

Attaining optimum yield or utility per recruit in the Queensland central coast mixed-species prawn fishery, or similar regional fisheries, appears to be unachievable using seasonal closures as a sole or major management tool. The complexity of recruitment dynamics, variation in species composition over quite small areas, and complexity of fleet dynamics mitigate against providing a single optimal starting date or duration. The best that could be hoped for in this type of fishery is a management regime that minimises capture costs and contains losses due to the capture of very small prawns from the most economically important species. Coastal, depth, or habitat-related closures in theory may be a more effective means of attaining these objectives than seasonal closures (Die and Watson 1992). Assessment of such alternatives would require further, more elaborate modelling.

Acknowledgments

The assessment of the 1988–91 east coast prawn trawling closure was funded by the Queensland Fish Management Authority. Data were kindly made available from the CFISH logbook database, run jointly by the Queensland Fish Management Authority and the Queensland Department of Primary Industries, Division of Fisheries and Wetlands Management. The authors thank the following people for their assistance. Staff of the Burnett Heads Fisheries Research Centre: Chris Lupton, Jeff Bibby, Brett Barr, Maureen Roll, and Lyn Wakefield, and the crew of the RV *Gwendolin May*: Phil Smith, Ian Withnall, and Paul Leeson.

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Appendix 1. Model Structure and Implementation

The model was deterministic with a resolution (step size) of 1 wk and accounted for differences in species, gender, timing, and relative strength of recruitment, growth, mortality, and size-dependent net selection. Yield was computed based on standard yield equations, formulated by length (size) class and in discrete time. Recruitment was defined as the number of prawns in a given size class that were at least partially susceptible to capture by commercial trawl nets. Instantaneous fishing mortality was allowed to vary with time and was assumed to be directly proportional to fishing effort (following Murawski 1984) (Fig. A1); such variation allowed the simulation of a pulse of fishing effort that occurred at the opening of the season. Fishing mortality was taken to involve all prawns retained by the net.

Table A1 details subscripts, parameters, and definitions used in the full model; Table A2 details the formulae used. For clarity, use of subscripts has been limited to l for length and size class and t for time interval.

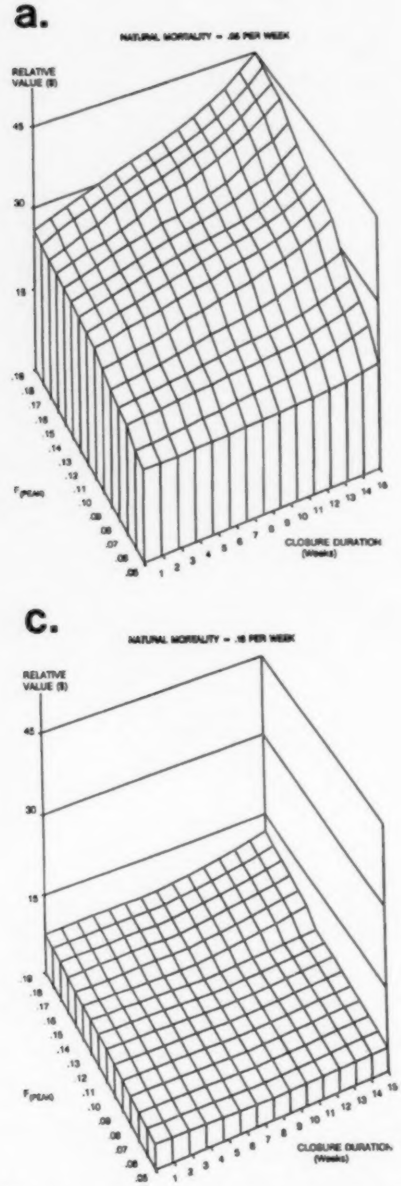

FIG. A1. Surface response plots of relative yield from simulation of the mixed-species prawn fishery in the Bowen/Mackay region under increasing natural mortality ($M = 0.05–0.20·wk^{-1}$). (*Fig. A1 concluded next page*)

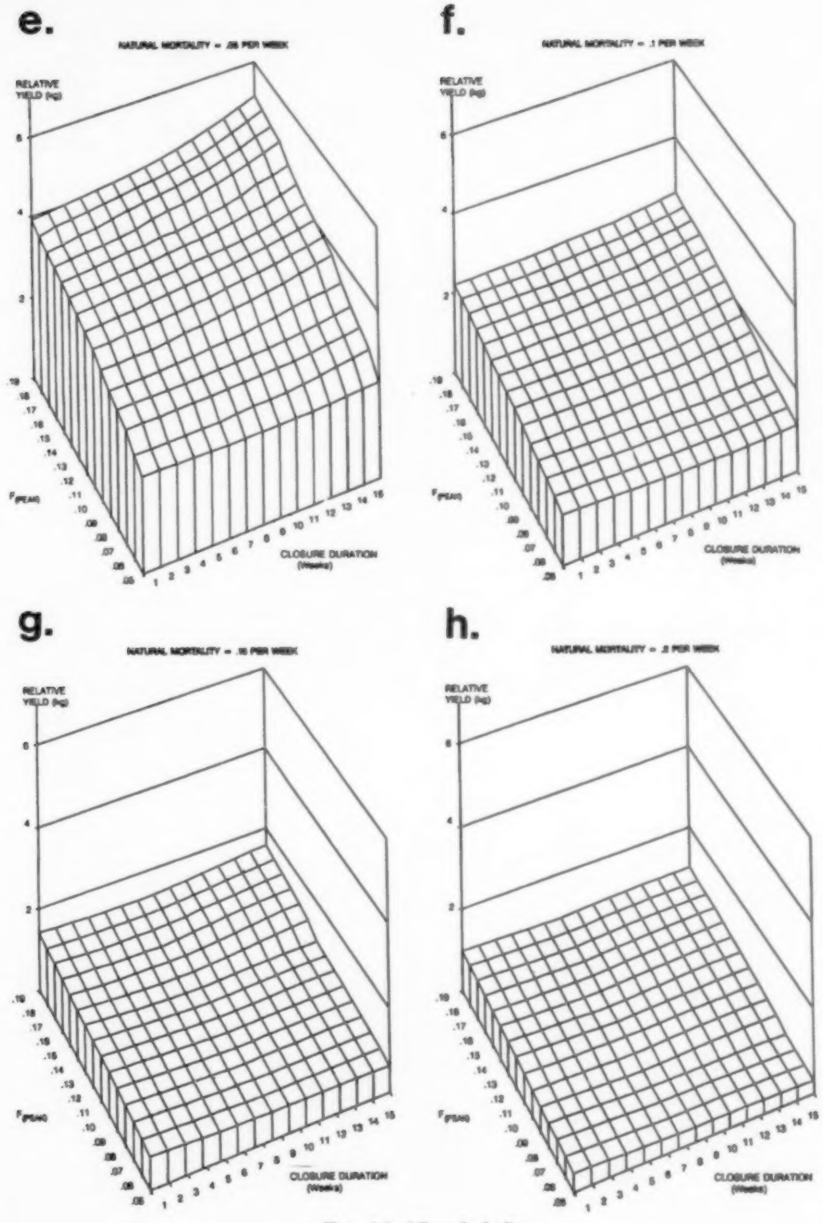

FIG. A1. (*Concluded*)

TABLE A1. Definition of referenced parameters and subscripts used in the text and the yield-per-recruit simulations of the Queensland central coast prawn fishery.

Parameter	Subscript	Definition
	c	Commercial size category (counts-per-pound) (see text)
	g	Gender
	l	Length size class (CL from 18 to 60 mm in 0.1-mm classes)
	s	Species (1–6)
	t	Time interval (wk)
a	s, g	Intercept of CL–weight relationship
b	s, g	Slope of CL–weight relationship
F	t	Fishing mortality
K	s, g	von Bertalanffy growth coefficient
L	s, g, t	Length at age (CL in mm)
L_∞	s, g	Length at infinity (CL in mm)
M	t	Natural mortality
N	s, g, t, l	Number of prawns
PR	s, g, t, l	Partial recruitment factor (see text)
RE	t	Proportion of fishing effort
S	s, g, t, l	Proportion of size class selected
$S1$	s, g, t, l	Net selection coefficient
$S2$	s, g, t, l	Net selection coefficient
SC	s	Proportion of catch per species
U	s, g, t, l	Dollar value (utility) per recruit
U_{TOT}		Total dollar value of simulation
V	s, c	Dollar value per commercial size category
W	s, g	Weight (g)
Y	s, g, t, l	Yield (g) per recruit
Y_{TOT}		Total yield (g) of simulation

TABLE A2. Formulae used for the yield-per-recruit and utility-per-recruit simulations of the Queensland central coast prawn fishery.

Gender-specific growth (size class):

$$L(t) = L_\infty \times (1 - e^{-K(t-t_0)})$$

$$t(L) = t_0 - \frac{1}{K} \ln \left[1 - \frac{L}{L_\infty} \right]$$

Instantaneous fishing mortality:

$$F_t = F \times PR_t$$

Partial recruitment factor "PR" (Murawski 1984):

$$\mathrm{PR}_t = S_{(l)t} \times \mathrm{RE}_t \times \mathrm{CL}_t$$

Ramped fishing effort "RE" (see text):

$$\mathrm{RE}_{(t+1)} = \mathrm{RE}_t - \left[\frac{\mathrm{RE}_{(\mathrm{MAX})}}{\mathrm{season}} \right]$$

Number of prawns per size class:

$$N_{(t+1)} = N_{(t)} [e^{(-M + F \times PR_t)}]$$

Yield-per-recruit:

$$Y(l)_t = \sum_l \left[N_t \times \frac{(F \times \mathrm{PR}_t)}{(F \times \mathrm{PR}_t + M)} \times [1 - e^{(F \times \mathrm{PR}_t + M)}] \times W_t \right]$$

Utility-per-recruit:

$$U_{lt} = \sum_4^0 W_{lt} \times V_c$$

Fully subscripted yield and utility models:

$$Y_{\mathrm{TOT}} = \sum_s \left[\mathrm{SC}_s \times \sum_g \sum_t \sum_l \left[N_{sgtl} \times \frac{(F \times \mathrm{PR}_{sgtl})}{(F \times \mathrm{PR}_{sgtl} + M_t)} \times [1 - e^{(F \times \mathrm{PR}_{sgtl} + M)}] \times W_{sgtl} \right] \right]$$

$$U_{\mathrm{TOT}} = \sum_s \left[\mathrm{SC}_s \times \sum_g \sum_t \sum_l \sum_c \left[N_{sgtlc} \times \frac{(F \times \mathrm{PR}_{sgtl})}{(F \times \mathrm{PR}_{sgtl} + M_t)} \times [1 - e^{(F \times \mathrm{PR}_{sgtl} + M_t)}] \times W_{sgtlc} \times V_{sc} \right] \right]$$

Comparative Survival and Growth of Two Strains of Atlantic Cod (*Gadus morhua*) through the Early Life Stages in a Marine Pond

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Blom, G., T. Svåsand, K.E. Jørstad, H. Otterå, O.I. Paulsen, and J.C. Holm. 1994. Comparative survival and growth of two strains of Atlantic cod (*Gadus morhua*) through the early life stages in a marine pond. Can. J. Fish. Aquat. Sci. 51: 1012–1023.

Survival and growth of two strains of Atlantic cod (*Gadus morhua*) were compared through the larval and juvenile stages in a marine pond in western Norway in 1990 and 1991. Strain A was homozygous for the genetic marker allele *GPI-1*30* at the glucose phosphate isomerase (GPI) locus expressed in white muscle, and Strain B possessed other *GPI-1** genotypes. In 1990 the frequency of Strain B increased significantly from the larval to the juvenile stage; however, in 1991 the frequency of Strain A increased slightly but not significantly from the larval to the juvenile phase. Larval mortality did not differ significantly between strains any year, but juvenile mortality was significantly lower in Strain B in 1990 and Strain A in 1991. Average growth rates in length estimated from regressions were not significantly different between strains during the larval and juvenile period any year, but initial length was significantly larger in Strain B in 1990 and Strain A in 1991. Our results indicated that food limitation during the early juvenile stage induced differential size-selective mortality among the strains due to small differences in body size and actual age between strains. Body size did not become important for survival until the food-limited regime had occurred.

Nous avons comparé la survie et la croissance de morues franches (*Gadus morhua*) de deux souches durant les stades larvaire et juvénile, qui étaient conservées dans un vivier situé dans le secteur ouest de la Norvège, en 1990 et en 1991. La souche A était homozygote à la position de l'allèle *GPI-1*30,* un marqueur génétique, soit au locus codant pour la glucose phosphate isomérase (GPI) exprimée dans le muscle blanc; la souche B possédait d'autres génotypes de *GPI-1**. En 1990, la fréquence de la souche B s'est accrue significativement entre le stade larvaire et le stade juvénile; toutefois, en 1991, la fréquence de la souche A s'est accrue légèrement, mais pas de manière significative, entre les mêmes stades. La mortalité au stade larvaire n'a pas différé significativement d'une souche à l'autre en aucune des deux années, mais la mortalité chez les juvéniles a été significativement moindre chez la souche B en 1990, et chez la souche A en 1991. La moyenne du taux de croissance en longueur estimée à partir de régressions durant la période larvaire comme durant la période juvénile n'a pas différé significativement entre les souches en aucune des deux années; cependant, la longueur initiale des sujets de la souche B était significativement supérieure en 1990 et celle des sujets de la souche A en 1991. Nos résultats montrent qu'une limitation d'ordre alimentaire au commencement du stade juvénile a provoqué une mortalité différentielle, entre les souches, qui était fonction de la taille et qui était attribuable à de petites différences de taille et d'âge réel entre les souches. La taille ne devenait pas un facteur important de survie avant la mise en oeuvre du régime de limitation des aliments.

Received April 7, 1993
Accepted November 23, 1993
(JB881)

Reçu le 7 avril 1993
Accepté le 23 novembre 1993

Accurate estimates of growth and particularly survival of cohorts of fish larvae are difficult to obtain due to ageing and sampling problems (e.g., Houde 1987). Thus, use of genetically marked fish larvae in release experiments provides a unique opportunity to study early life dynamics and recruitment mechanisms (Jamieson 1974; Shaklee 1983; Svåsand et al. 1991). The important parameters, size, age, and abundance of fish larvae at release are then known. In 1988, a preliminary release experiment with genetically marked Atlantic cod larvae (*Gadus morhua*) was carried out in a small land-locked fjord in western Norway, and survival was estimated at 3.3% in the late larval stage (Svåsand et al. 1991).

Maternal influence on the quality of eggs and larvae may be a factor that affects recruitment potential (Montelone and Houde 1990; Kjesbu et al. 1992). Generally, larger females produce larger eggs which produce larger larvae at hatching (Hislop 1988; Kjesbu 1989; Zastrow et al. 1989; Monteleone and Houde 1990; Buckley et al. 1991b; Kjesbu et al. 1992). Miller et al. (1988) concluded that survival of species with small progeny should be more variable than the survival of species with larger progeny due to increased vulnerability to starvation and predation with decreasing size. Even subtle differences in size between individuals may have profound effects on their fates (Miller et al. 1988). Size-dependent survival during the early stages may be

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TABLE 1. Sex distribution and comparisons (t-tests) of mean length, weight, and Fulton's condition factor (K = (weight/length^3)100 000) of mature Atlantic cod from two broodstocks (A and B) in 1990 (measured in the beginning of December 1989) and 1991 (measured in the beginning of February 1991). SD's are given in parentheses.

Broodstock	n	Length (cm)	Weight (kg)	Fulton's K
1990				
♀				
A	90	64 (5.2)	4.4 (1.0)	1.66 (0.20)
B	58	72 (12.3)	5.9 (2.4)	1.55 (0.22)
Prob.		A < B; $p < 0.001$	A < B; $p < 0.001$	A > B; $p < 0.001$
♂				
A	113	62 (5.8)	3.6 (1.0	1.47 (0.16)
B	58	72 (11.7)	5.4 (2.3)	1.35 (0.16)
Prob.		A < B; $p < 0.001$	A < B; $p < 0.001$	A > B; $p < 0.001$
1991				
♀				
A	51	68 (5.9)	4.9 (1.2)	1.55 (0.18)
B	116	58 (4.4)	3.6 (0.8)	1.79 (0.32)
Prob.		A > B; $p < 0.001$	A > B; $p < 0.001$	A < B; $p < 0.001$
♂				
A	80	67 (5.9)	4.0 (1.0	1.29 (0.15)
B	75	58 (5.1)	3.0 (0.8)	1.53 (0.21)
Prob.		A > B; $p < 0.001$	A > B; $P < 0.001$	A < B; $p < 0.001$

directly related to growth (Anderson 1988), and small changes in daily growth or mortality rates of fishes may cause major changes in recruitment levels, especially if they occur in the larval stage (Houde 1987).

Shepherd and Cushing (1980) suggested that the abundance of food per larva resulted in density-dependent growth which interacted with predation to produce density-dependent larval survival. Actually, the regulation of the numbers may be density independent in the larval stage because of the little impact larvae have on the abundance of their prey (Houde 1987; Fortier and Harris 1989; Economou 1991; Jenkins et al. 1991). But density-dependent control of numbers probably does apply in the juvenile stage (Houde 1987).

Recently, a genetically marked broodstock of Atlantic cod was developed at the Institute of Marine Research (Jørstad et al. 1987; Skaala et al. 1990; Jørstad et al. 1991). These fish were homozygous for the rare allele *GPI-1*30* in the enzyme glucose phosphate isomerase (GPI) expressed in white muscle. The homozygote, *GPI-1*30/30*, can be identified from the yolk-sac stage (Jørstad et al. 1987, 1991).

The aim of this study was to examine the effects of differences in egg and larval size and age on growth and survival of early life stages of Atlantic cod. This was achieved by releases of two strains (A and B) of cod larvae into a marine pond and where Strain A was homozygous for the genetic marker allele *GPI-1*30* and Strain B possessed other *GPI-1** genotypes.

Materials and Methods

Broodstock Characteristics and Production of Eggs and Larvae

Two different broodstocks (A and B) of Atlantic cod kept at the Austevoll Aquaculture Research Station in western Norway were used for egg production. Broodstock A was homozygous for the *GPI-1*30* allele, and Broodstock B was a farmed cod stock with other *GPI-1** genotypes. The *GPI-1*30* allele is present in heterozygous forms at a frequency between 0.01 and 0.05 in wild cod populations in Norway (Jørstad et al. 1991; Gjøsæter et al. 1992). In 1990, both sexes from Broodstock B were significantly longer and heavier than those from Broodstock A and vice versa in 1991 (Table 1). However, the mean condition factors of adults from Broodstock A were significantly higher than those of adults from Broodstock B in 1990 and vice versa in 1991 (Table 1).

In early February 1990 and 1991, the two broodstocks were transferred into separate 175-m^3 polyethylene floating pens where they spawned naturally, and fertilized eggs were collected as described by Holm and Andersen (1989). Progeny from Broodstock A and Broodstock B were termed Strain A and Strain B, respectively. The fertilized eggs were treated in a 1% solution of Buffodine (Evans Vanodine International Ltd., England) and incubated in 180-L, aerated, black, conical tanks. Mean incubation temperature was 6.7°C (range 5.7–8.6°C) and 5.1°C (range 4.1–5.9°C) in 1990 and 1991, respectively, and mean salinity was 33.6 ppt (range 33.0–34.0 ppt) and 33.0 ppt (range 32.7–33.5 ppt) in 1990 and 1991, respectively.

Pond Description and Rearing Routines

The marine pond, called Parisvatnet, is situated at 60°38′N, 4°49′E, 60 km northwest of Bergen, Norway. The pond has a maximum depth of 9 m, a surface area of 50 000 m^2, and a volume of 270 000 m^3. Further descriptions of the pond and rearing routines are given in Blom et al. (1991) and in Table 2.

In 1990, a total of 11.1 million (SD = 0.93 million) eggs and larvae were released between 16 and 22 March, and 79.9% (SD = 7.9%) and 20.1% (SD = 2.7%) of the specimens were Strain A and Strain B, respectively (Table 3). In 1991, a total of 7.1 million (SD = 0.71 million) eggs and larvae were released, and 45.2% (SD = 7.8%) and 54.8% (SD = 6.2%) of the specimens were Strain A and Strain B, respectively

TABLE 2. Overview of different rearing procedures carried out in Parisvatnet in 1990 and 1991. DW = dry weight.

Procedures	1990	1991
Stagnant period	16 March – 30 April	23 March – 13 May
Fertilization with inorganic fertilizer (kg)[a]	10 March: 200; 2 April: 100	15 March: 100; 26 March: 50; 3 April: 50; 16 April: 50
Supply of tidal water	30 April – 21 May: 1.5-mm screens; From 21 May: 2.0-mm screens	From 13 May: 2.0-mm screens
Supply of sea water from 30 m depth with an electrical pump (capacity 10 $m^3 \cdot min^{-1}$)	From 31 May	From 31 May
Supply of zooplankton (kg DW) collected with a fine-meshed trawl (opening area 25 m^2)	25 April – 29 May: <2	30 April – 31 May: 6–25 (mainly *Calanus*)
Supply of zooplankton (kg DW) collected with a zooplankton concentrator (capacity 30 $m^3 \cdot min^{-1}$)		2 May – 1 June: 0.6–3.0 (mainly *Calanus*)
Supply of formulated dry feed	From 25 April	From 10 May

[a] Chemical composition (%) in weight for important elements in the inorganic fertilizer: N, 21.0; P, 3.5; K, 10.5; Si, 0.5–1.0.

TABLE 3. Releases of Atlantic cod eggs and larvae from two strains in Parisvatnet in 1990 and 1991 and estimated days after hatching (DAH) assuming an interval of 2 d from 50 to 100% hatching at ambient temperatures. SD's and number of samples are given in parentheses.

	Strain A		Strain B	
Date	Eggs and larvae (thousands)	DAH	Eggs and larvae (thousands)	DAH
1990				
16 March	1959 (265; 6)	1.9	1381 (269; 6)	1.9
17 March	1537 (333; 5)	1.9	86 (7; 3)	1.9
18 March	559 (105; 5)	1.7	764 (131; 5)	1.9
21 March	1836 (102; 6)	0.9		
22 March	2991 (756; 6)	−0.3		
Total	8882		2231	
1991				
23 March	646 (162; 5)	2.0	1426 (350; 5)	1.9
24 March	949 (281; 5)	1.8	275 (28; 5)	1.8
25 March	1601 (448; 5)	1.5	2174 (254; 5)	1.9
Total	3196		3875	

(Table 3). The arithmetic mean dates of 50% hatching (Day 0) was 17 March (Strain A: 14 March; Strain B: 18 March) and 22 March (Strain A and Strain B: 22 March) for the total population in 1990 and 1991, respectively.

Sampling Programme

Temperature, salinity, and oxygen saturation were monitored weekly in the pond at 1-m depth intervals from the surface to the bottom.

Microzooplankton was sampled weekly by using an electrical pump of 72 $L \cdot min^{-1}$ capacity and filtered through a net of 30-μm mesh size. The samples were collected at different depths (1990: 1, 4, 5, 7 m, and 10 cm above the bottom; 1991: 1, 2, 3, 4, 5, 6, 7 m, and 10 cm above the bottom) at one sampling site (8.5 m depth). Macrozooplankton and cod larvae used for abundance estimates were sampled at night (21:00–01:00) once a week with a two-chambered net (mesh size 350 μm; mouth area 2 × 0.05 m^2) (Kvenseth and Øiestad 1984; Blom et al. 1991; van der Meeren and Næss 1993). The net was towed horizontally at a speed of 1 $m \cdot s^{-1}$ at depth intervals of 1 m to a depth of 8 m. Zooplankton and cod larvae were preserved in 96% ethanol. Abundance of juvenile cod (≥Day 48) was estimated with a 200-kHz Furuno echo sounder at night (24:00–01:30). Echo sounder surveys were conducted on 18 and 23 May and 19 June in 1990 (one estimate on each day) and on 9 May (one estimate) and 8 June (three estimates) in 1991. Standing stocks of micro- and macrozooplankton and larval and juvenile cod were calculated by multiplying density estimates by water volume allocated to each depth stratum. Metamorphosis in cod was defined as the age after hatching that the larval median finfold disappears, i.e., about 12 mm standard length (Pedersen and Falk-Petersen 1992).

Live larval samples for identification of different *GPI-1** genotypes were collected from the pond with the two-chambered net described above during the day, except for the sample taken on 29 April 1991 which was collected at 23:30. Live juvenile samples were collected from the pond with a dip net during the day. The dip net with a diameter of 10 m was mounted to a steel frame which was connected to a crane equipped with a hydraulic winch. Before sampling, the dip net was lowered to the bottom of the pond, dry feed was offered from an automatic feeder, and the dip net was lifted to the surface and confined the juvenile cod which had aggregated to eat the dry feed. The samples collected on 4 and 8 October 1990 and 30 July, 1 August, and 13 August 1991 were taken randomly and in accordance with the number of individuals in each of three and six 100-m^3 net pens, respectively, stocked with thousands of juvenile cod. These cod constituted the harvest of juveniles from the pond, and they were captured with the dip net described above (about 80% of the total catch), a 100-m-long shore seine (about 10% of the total catch) and a 225-m^2 sink seine (about 10% of the total catch) from the beginning of June. Cumulatively, 50% total juvenile catch was passed on 3 July 1990 and 28 June 1991 which were used as reference points for the total juvenile harvest in these years. The juvenile cod were size graded and vaccinated against vibriosis before being kept in the net pens where they were offered dry feed in excess.

For genetic analyses, whole larvae or a small amount of white muscle from juveniles was frozen at −70°C within a few hours of sampling and later analysed by horizontal starch gel electrophoresis for identification of *GPI-1** genotypes (Jørstad et al. 1991).

A *G*-test (log likelihood ratio test) was used to compare the strain frequencies during the larval and juvenile stages (Sokal and Rohlf 1981).

Estimation of Mortality and Growth

A survival curve of cod was constructed from pooled (two subsequent samplings) and single population estimates including the estimate of total juvenile catch, and instantaneous daily mortality rates (z) during the intervals were calculated. Separate z's of Strain A and Strain B were estimated from release to the late larval stage, and from the late larval stage to 50% total juvenile catch based on numbers from the survival curves and strains frequencies within periods.

Growth rates of the strains were estimated from the pond, applying the regression

$$(1) \quad \ln SL_t = \ln SL_0 + gt$$

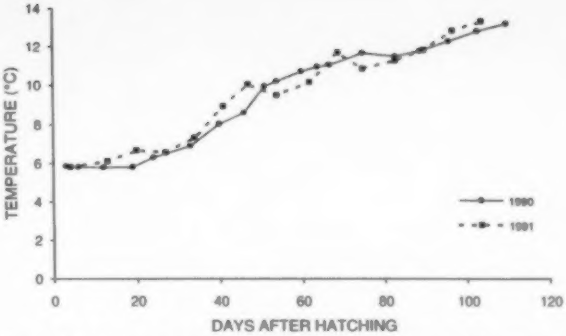

FIG. 1. Mean temperature in Parisvatnet in 1990 and 1991. Day 0 corresponds to 17 March in 1990 and 22 March in 1991.

where SL_t is live standard length (millimetres) at time t, SL_0 is live standard length (millimetres) at hatching, g is the instantaneous daily growth coefficient, and t is days after hatching.

Results

Hydrography

The temperature regimes in the pond were similar both years with mean temperatures ranging from 5.8 to 13.4°C (Fig. 1). In 1990, the average salinity ranged from 27.5 to 32.9 ppt and from 30.1 to 33.2 ppt in 1991, and the salinity was lowest towards the end of the stagnant period. The average oxygen levels in the pond were generally higher in 1991 than in 1990 with values varying from 9.9 to 12.3 ppm in 1990 and from 11.7 to 12.8 ppm in 1991.

Zooplankton

In 1990, the average density of microzooplankton in the pond varied between 2.0 and $150 \cdot L^{-1}$ from Day 6 to 54, with the maximum density on Day 19 (Fig. 2a). The mean abundances of copepod nauplii varied between 0.9 and $6.0 \cdot L^{-1}$ from Day 6 to 54. Between Days 4 and 62 in 1991, the mean density of microzooplankton ranged from 1.6 to $124 \cdot L^{-1}$ (Fig. 2b), with the maximum abundance on Day 39, and copepod nauplii varied between 1.4 and $20 \cdot L^{-1}$. Larvae of the blue mussel (*Mytilus edulis*) were numerically dominant among microzooplankters both years. The mean density of macrozooplankton increased from $99 \cdot m^{-3}$ on Day 5 to a maximum of $670 \cdot m^{-3}$ on Day 24 and declined rapidly to only $3.0 \cdot m^{-3}$ on Day 62 in 1990 (Fig. 2c). In 1991, the average density of macrozooplankton ranged from 513 to $1412 \cdot m^{-3}$ between Days 4 and 39, and on Day 62 the density was <4.0 macrozooplankton$\cdot m^{-3}$. Copepodites of the calanoid copepods *Temora longicornis*, *Centropages hamatus*, and *Calanus finmarchicus* (almost absent in 1990) dominated numerically among macrozooplankters in the pond both years.

Size of Eggs and Yold-sac Larvae

Generally, eggs from Strain A were significantly smaller in diameter than eggs from Strain B in 1990, although the differences were small (Table 4a). There was no significant difference in SL of individuals from Strain A and Strain B at release (Table 4b), but the mean dry weight (DW) of lar-

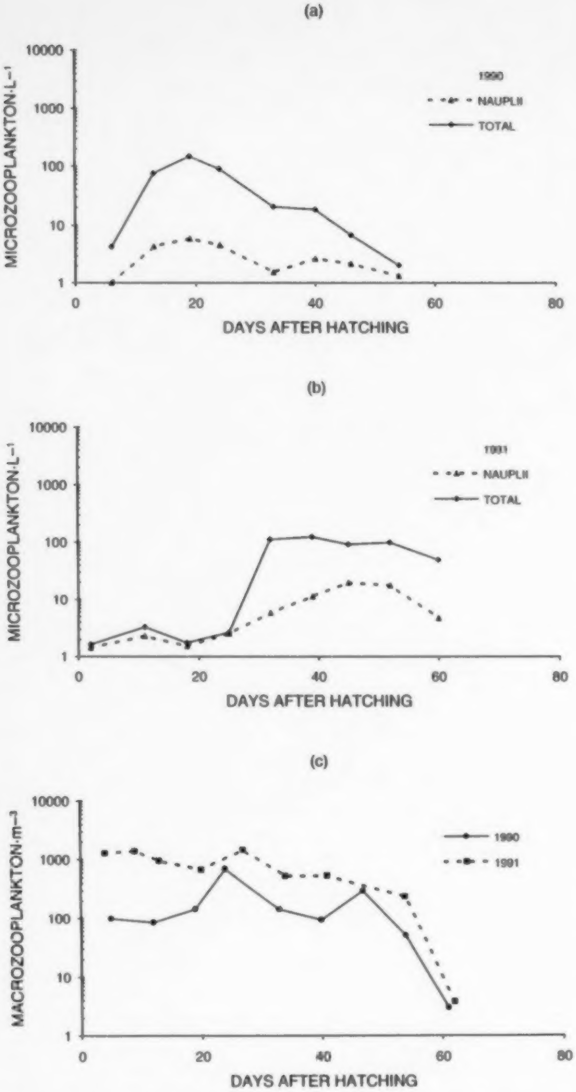

FIG. 2. Mean densitites of microzooplankton in (a) 1990 and (b) 1991 and (c) macrozooplankton in 1990 and 1991 in Parisvatnet. Day 0 corresponds to 17 March in 1990 and 22 March in 1991.

vae from Strain A was significantly lower than that of larvae from Strain B at release. In 1991, pooled weighted egg data demonstrated that the diameter of eggs from Strain A was significantly larger than that of eggs from Strain B. Pooled weighted data showed that the mean size (both SL and DW) of larvae did not differ significantly between strains at release.

Survival and Growth

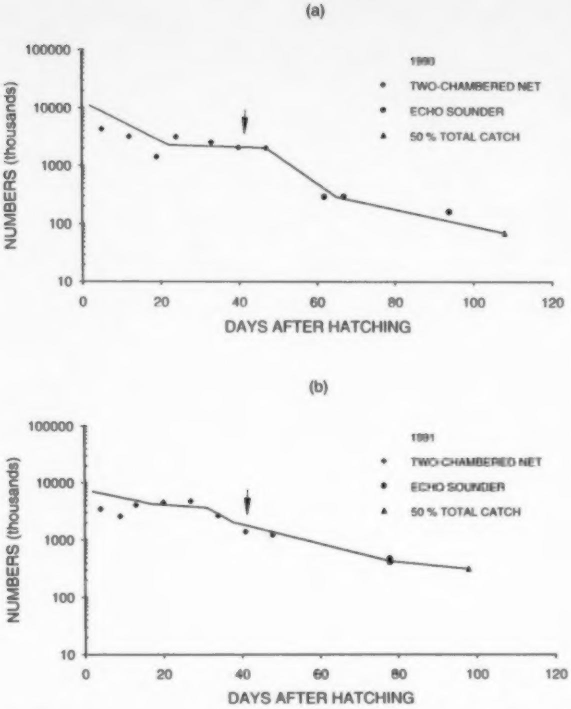

FIG. 3. Estimated survival curves for Atlantic cod fitted to the observed data from Parisvatnet in (a) 1990 and (b) 1991. The estimated instantaneous daily mortality rates (z) employed in the survival curves were 0.08 (Days 2–22), 0.005 (Days 22–47), 0.11 (Days 47–65), and 0.03 (Days 65–108) in 1990 and 0.03 (Days 2–17), 0.01 (Days 17–31), 0.09 (Days 31–38), 0.04 (Days 38–78) and 0.02 (Days 78–98) in 1991. The first two population estimates after release were regarded as underestimates because larvae concentrated close to the bottom of the pond and were then unavailable for sampling by the two-chambered net. Hence, these estimates were omitted when constructing the survival curves. The arows indicate time at metamorphosis. Day 0 corresponds to 17 March in 1990 and 22 March in 1991.

In 1990, the population decreased from 11.1 million eggs and larvae at release to 2.1 million larvae at metamorphosis (around Day 42), giving an estimate of 19% survival to metamorphosis (Fig. 3a). On Day 94, the number of juvenile cod was estimated at 161 000 individuals by echo sounder, giving an estimated survival of 7.7% from Day 42 to 94. A total of 71 000 juvenile cod were collected from the pond from the beginning of June to the end of October, resulting in an overall survival estimate of 3.4% from Day 42 to 108.

In 1991, the population declined from 7.1 million individuals at release to 1.7 million individuals at metamorphosis (around Day 42), leading to an estimate of 25% survival to metamorphosis (Fig. 3b). On Day 78, the number of juvenile cod was estimated at 433 000 individuals by echo sounder, giving an estimated survival of 25% survival from Day 42 to 78. Altogether, 317 000 juvenile cod were harvested from the pond from the beginning of June to the end of October, resulting in an overall survival estimate of 18% from Day 42 to 98.

Approximately 20% of the individuals were Strain B during the larval phase in 1990 (Fig. 4a), but this increased markedly to between 51.6 and 62.2% during the juvenile period. The frequencies of the strains changed from the lar-

TABLE 4. Comparisons (*t*-tests) of mean egg and larval sizes from two strains of Atlantic cod in 1990 and 1991. (a) Egg diameter (±0.04 mm) of fertilized eggs from the spawning pens on different dates. (b) Standard length (SL; ±0.08 mm) and dry weight (DW; 60°C, 24 h, ±1 μg) of cod larvae at release. Three samples (preserved in 10% hexamine-buffered formalin) and six samples (preserved in 96% ethanol) of larvae from the two strains were taken in 1990 and 1991, respectively. SD's and sample sizes are given in parentheses. NS: not significant.

Spawning date	Strain A	Strain B	Prob.
(a) Egg diameter			
1990			
28 February	1.31 (0.06; 40)	1.37 (0.05; 40	A < B; $p < 0.001$
1 March	1.38 (0.05; 40)	1.38 (0.07; 40)	NS
2 March	1.34 (0.06; 40)	1.39 (0.05; 40)	A < B; $p < 0.001$
7 March	1.34 (0.06; 40)		
8 March	1.37 (0.05; 40)		
9 March	1.33 (0.07; 40)		
Pooled (weighted)	1.34 (0.06; 240)	1.38 (0.05; 120)	A < B; $p < 0.001$
1991			
5 March	1.39 (0.05; 28)	1.39 (0.07; 28)	NS
6 March	1.38 (0.04; 40)	1.36 (0.04; 40)	A > B; $p < 0.05$
7 March	1.37 (0.05; 40)	1.33 (0.08; 40)	A > B; $p < 0.05$
Pooled (weighted)	1.37 (0.05; 108)	1.36 (0.07; 108)	A > B; $p < 0.05$
(b) Standard length and dry weight			
1990			
16–18 March			
SL (mm) pooled	4.21 (0.22; 100)	4.25 (0.25; 50)	NS
DW (μg) pooled	44.64 (6.64; 92)	48.21 (7.80; 47)	A < B; $p < 0.01$
1991			
SL (mm)			
23 March	4.47 (0.18; 100)	4.37 (0.18; 100)	A > B; $p < 0.001$
24 March	4.33 (0.20; 100)	4.27 (0.19; 100)	A > B; $p < 0.05$
25 March	4.31 (0.17; 90)	4.35 (0.15; 100)	A < B; $p < 0.05$
Pooled (weighted)	4.35 (0.18; 290)	4.35 (0.17; 300)	NS
DW (μg)			
23 March	37.50 (4.44; 86)	36.11 (4.63; 79)	NS
24 March	39.39 (4.41; 77)	39.38 (4.68; 85)	NS
25 March	39.89 (6.76; 87)	39.75 (7.57; 76)	NS
Pooled (weighted)	39.27 (5.72; 250)	38.39 (6.45; 240)	NS

val to the juvenile period (*G*-test; $p < 0.001$), but did not vary between strains within each of the periods (*G*-test; $p > 0.05$). In 1991, the proportion of Strain A ranged between 40.6 and 55.5% during the larval stage and between 53.1 and 59.7% during the juvenile stage (Fig. 4b). The frequencies of the strains varied between samples (*G*-test; $p < 0.01$). But as there were four homogeneous subsets with data from both the larval and the juvenile period, we conclude that there was a slight but not significant change in frequencies between strains from the larval to the juvenile stage.

In 1990, there was no difference in mean instantaneous daily mortality rate (z) between strains from release to the late larval stage (*t*-test; $p = 0.41$) (Table 5); however, the mean z of Strain A was higher than that of Strain B from the late larval stage to 50% total juvenile catch (*t*-test; $p < 0.0001$). Strain A had a higher mean z in the juvenile phase than in the larval phase (*t*-test; $p < 0.016$); however, in Strain B, there was no difference in mean z between the larval and the juvenile stage (*t*-test; $p = 0.06$). Mean z did not differ between strains from release to the late larval stage in 1991 (*t*-test; $p = 0.56$) (Table 5) but was lower in Strain A than in Strain B from the late larval stage to 50% total juvenile catch (*t*-test; $p < 0.003$). There was no differences in mean z between the larval and the juvenile period in either of the strains (*t*-test; $p > 0.06$). The mean z of Strain A was higher both in the larval stage (*t*-test; $p < 0.025$) and in the juvenile stage (*t*-test; $p < 0.0001$) in 1990 than in 1991, but there were no differences in mean z of Strain B either in the larval phase (*t*-test; $p = 0.14$) or in the juvenile phase (*t*-test; $p = 0.30$) between years.

In 1990, the average size (length and weight) of individuals from Strain A was significantly less than those from Strain B in all samples, except for Day 203 (Table 6). The mean size of individuals from Strain A was greater than those from Strain B in 1991; however, differences were significant only in three of six length samples and one of three weight samples. The length ratios between the 5% largest and 5% smallest individuals and coefficients of variation (CV) of lengths within each strain increased from the late larval stage and levelled off during the juvenile stage (Table 7). Generally, Strain B had larger variation in length ratios and

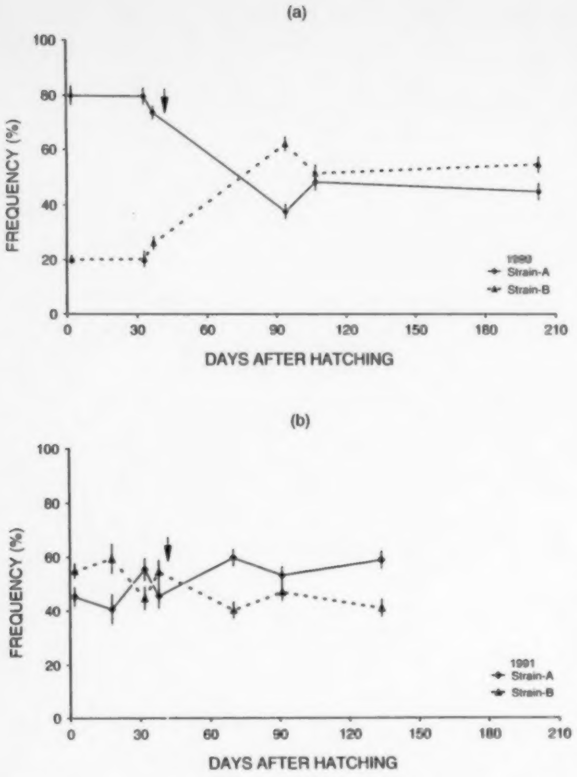

FIG. 4. Frequency (±SE) of two strains of Atlantic cod in Parisvatnet during the larval and juvenile stage in (a) 1990 and (b) in 1991. The arrows indicate time at metamorphosis. Day 0 corresponds to 17 March in 1990 and 22 March in 1991.

higher CV's than did Strain A both years. There was no significant difference in instantaneous growth coefficients (*g*) between strains based on SL data from 1990 (analysis of covariance (ANCOVA); $p = 0.08$) and 1991 (ANCOVA; $p = 0.26$) (Table 8). However, the intercepts (ln SL_0) were different between strains both years (ANCOVA; $p < 0.001$).

TABLE 5. Instantaneous daily mortality rates (*z*) of two strains of Atlantic cod during the periods from release to the late larval stage and from the late larval stage to 50% total juvenile catch in Parisvatnet in 1990 and 1991. The mortality rates were estimated from the survival curves and strain frequencies presented in Fig. 3 and 4, respectively. The strain frequencies did not change significantly within the larval or juvenile period and were thus treated as independent estimates. Day 0 corresponds to 17 March in 1990 and 22 March in 1991.

		z ± SD	
Period	*n*	Strain A	Strain B
1990			
Days 2–37	2	0.048 ± 0.002	0.044 ± 0.005
Days 37–108	3	0.056 ± 0.002	0.036 ± 0.001
1991			
Days 2–38	3	0.034 ± 0.004	0.036 ± 0.004
Days 38–98	3	0.028 ± 0.001	0.034 ± 0.001

Discussion

In spite of a total mortality of 81 and 75% during the larval period in 1990 and 1991, respectively, no significant changes in the frequency of genetically marked cod (Strain A) were noticed. Nor did the mean instantaneous daily mortality rate differ significantly between strains during the larval phase any year. But the frequency of Strain A decreased significantly postmetamorphosis in 1990 and increased slightly but not significantly postmetamorphosis in 1991. The mean instantaneous mortality of Strain A was significantly higher than that of Strain B during the juvenile period in 1990 and significantly lower than that of Strain B during the juvenile period in 1991. These changes in survival patterns coincided with the increased mortality rates of the populations around and after metamorphosis (Fig. 3 and 4). The effect of selection for size should be most noticeable when mortality is highest (Rosenberg and Haugen 1982), which is supported in our study. First, Strain A had a significantly smaller body length than Strain B at the late larval stage (Day 37) in 1990 and significantly larger body length at the late larval stage (Day 38) than Strain B in 1991. The length ratios between the largest and smallest individuals at the late larval stage had reached levels (>1.5) both within and between strains required for cannibalism to occur (Folkvord 1993; Folkvord and Otterå 1993). Second, the majority of larvae from Strain A must have started exogenous feeding on average 4 d later than larvae from Strain B in 1990 due to the difference in hatching time between strains. Thus, size-selective mortality most likely due to cannibalism might be a reasonable explanation for the significant decrease of Strain A postmetamorphosis in 1990 and the slight increase of Strain A postmetamorphosis in 1991. Generally, cannibalism in fishes tends to increase with increasing density and decreasing food availability; however, its role in population regulation has not been unequivocally demonstrated in any wild population (Smith and Reay 1991). Size-selective mortality due to cannibalism has been documented under intensive and extensive rearing conditions (Loadman et al. 1986; Katavić et al. 1989; Folkvord 1991; Otterå and Lie 1991; Parazo et al. 1991; Folkvord 1993; Folkvord and Otterå 1993) and in wild fish populations (Loadman et al. 1986; Bailey 1989; Koeller et al. 1989; Tsukamoto et al. 1989). Otterå and Folkvord (1993) found that cod juveniles of about 20 mm had the lowest potential predator/prey length ratio (1.3) based on mouth gape of the predator and the body height of the prey. This implies that the cannibalistic potential is maximised in this size range.

Growth and survival of young fish are thought to be affected by density-dependent processes such as competition for food and predation including cannibalism (Ware 1975; Shepherd and Cushing 1980; Smith 1985; van der Veer 1986; Koeller et al. 1989; Blom et al. 1991; Trebitz 1991), but direct evidence for the existence of density-dependent competition for food in fish larvae is sparse (Kiørboe et al. 1988; Fortier and Harris 1989; Fortier and Gagné 1990; Young and Davis 1990; Economou 1991; Jenkins et al. 1991; McGurk et al. 1993). However, density-dependent mechanisms might first become important in the stages following the larval stage (van der Veer 1986; Anderson 1988; Suthers

TABLE 6. Comparisons (*t*-tests) of mean standard lengths (SL) and wet weights (WW) of Atlantic cod from two strains related to days after hatching (DAH) in Parisvatnet in 1990 and 1991. SD's and sample sizes are given in parentheses. Day 0 corresponds to 17 March in 1990 and 22 March in 1991. NS: not significant.

	SL (mm)			WW (g)		
DAH	Strain A	Strain B	Prob.	Strain A	Strain B	Prob.
1990						
37	9.98 (0.88; 280)	10.30 (0.89; 100)	A < B; $p < 0.01$			
94	51.28 (7.85; 145)	54.42 (9.01; 239)	A < B; $p < 0.001$	1.49 (0.72; 144)	1.86 (1.05; 239)	A < B $p < 0.001$
107	52.96 (4.73; 139)	54.52 (4.99; 148)	A < B; $p < 0.01$	1.61 (0.52; 138)	1.75 (0.60; 148)	A < B $p < 0.05$
203[a]	156.6 (22.3; 141)	159.4 (25.3; 172)	NS	39.99 (20.57; 141)	43.80 (23.87; 172)	NS
1991						
18	5.68 (0.43; 39)	5.41 (0.62; 57)	A > B; $p < 0.05$			
32	8.61 (0.81; 93)	8.44 (0.74; 75)	NS			
38	9.85 (0.77; 66)	9.39 (0.89; 79)	A > B; $p < 0.01$			
70	42.25 (6.38; 172)	42.32 (7.69; 116)	NS	0.78 (0.35; 172)	0.81 (0.59; 116)	NS
91	46.70 (7.19; 153)	46.25 (7.69; 135)	NS	1.08 (0.62; 153)	1.07 (0.91; 135)	NS
134[a]	96.0 (14.1; 148)	92.0 (14.3; 103)	A > B; $p < 0.05$	9.43 (3.99; 148)	8.27 (3.73; 102)	A > B; $p < 0.05$

[a] Total length was measured.

TABLE 7. Range of standard lengths (SL) of the 5% smallest (S) and 5% largest (L) individuals, range of length ratios (L/S) between these groups, and coefficient of variation (CV) for standard lengths of Atlantic cod from two strains related to days after hatching (DAH) in Parisvatnet in 1990 and 1991. Data for measured SL's of larvae at release (Day 2) were corrected for shrinkage in formalin (1990) and ethanol (1991) by using the following relationships between live SL and preserved SL given by Hjörleifsson and Klein-MacPhee (1992): $SL_{live} = 0.47 + 1.02\ SL_{formalin}$ and $SL_{live} = 0.41 + 0.94\ SL_{ethanol}$. Data for measured total lengths (TL) on Day 203 in 1990 and on Day 134 in 1991 were transformed to SL by the relationship $SL = -0.46 + 0.93\ TL$; $r^2 = 1.0$; $n = 60$ (G. Blom, unpublished data). Day 0 corresponds to 17 March in 1990 and 22 March in 1991.

	Strain A				Strain B			
DAH	S (mm)	L (mm)	L/S	CV (%)	S (mm)	L (mm)	L/S	CV (%)
1990								
2	4.03–4.37	5.13–5.29	1.17–1.31	4.6	4.11–4.45	5.21–5.47	1.17–1.33	5.3
37	8.00–8.70	11.50–13.00	1.32–1.63	8.8	8.20–8.80	12.00–12.70	1.36–1.55	8.8
94	33.5–38.0	64.5–77.5	1.70–2.31	15.3	34.0–41.0	71.0–88.0	1.73–2.59	16.6
107	40.5–46.5	60.5–70.0	1.30–1.73	8.9	42.5–48.0	62.0–78.0	1.29–1.84	9.2
203	98.8–110.0	180.5–217.6	1.64–2.20	14.3	100.7–110.0	189.8–200.9	1.73–2.00	15.9
1991								
2	3.86–4.25	4.80–4.99	1.13–1.29	4.0	3.62–4.25	4.72–5.03	1.11–1.39	3.8
18	4.58–5.00	6.41–6.50	1.28–1.42	7.6	4.17–4.33	6.33–6.83	1.46–1.64	11.4
32	7.01–7.52	10.02–11.02	1.33–1.57	9.4	6.68–7.01	9.69–10.02	1.38–1.50	8.7
38	7.83–8.83	11.17–12.00	1.27–1.53	7.8	7.17–7.83	10.38–11.67	1.38–1.63	9.5
70	28.0–30.0	51.0–54.0	1.70–1.93	15.1	29.5–31.0	53.0–69.0	1.71–2.34	18.2
91	32.0–35.0	59.0–77.0	1.69–2.41	15.4	32.0–37.0	55.5–73.0	1.50–2.28	16.6
134	51.9–64.9	109.5–115.0	1.69–2.22	14.7	49.1–59.3	103.9–118.7	1.75–2.42	15.6

et al. 1989; Blom et al. 1991; Bradford 1992). In our study, the density of macrozooplankton declined rapidly post-metamorphosis due to cod predation and remained low during the early juvenile stage both years. A rapid increase in the food demand of cod after metamorphosis was demonstrated by Blom et al. (1991). The total density of microzooplankton peaked around metamorphosis in 1991, i.e., about 20 d later than in 1990. But the density of copepod nauplii peaked after metamorphosis in 1991, indicating improved recruitment to the youngest copepodite stages which were not properly sampled with the 350-μm-mesh two-chambered net. The supply of zooplankton with dif-

TABLE 8. Statistics of ln SL regressed on days after hatching for two strains of Atlantic cod collected from Parisvatnet during the larval and juvenile period in 1990 and 1991. SL_0 is live standard length (mm) at hatching and g is the instantaneous daily growth coefficient. Length data for juveniles collected from the net pens were omitted from the regression. Data for measured SL's of larvae on Day 2 were corrected for shrinkage as shown in Table 7.

Strain	n	ln SL_0 ± SE	g ± SE	r^2	Prob.
1990					
A	664	1.438 ± 0.010	0.0247 ± 0.0001	0.977	$p < 0.0001$
B	541	1.480 ± 0.012	0.0252 ± 0.0002	0.957	$p < 0.0001$
1991					
A	813	1.406 ± 0.012	0.0287 ± 0.0002	0.954	$p < 0.0001$
B	762	1.381 ± 0.011	0.0284 ± 0.0002	0.953	$p < 0.0001$

ferent filtering systems was about one order of magnitude higher in 1991 than in 1990 (see Table 2). Thus, we conclude that the total food availability must have been better during the early juvenile stage in 1991 than in 1990 and that the conditions for density-dependent food competition and cannibalism may have been present, especially in 1990 (Øiestad et al. 1985; Blom et al. 1991; Folkvord 1993). These density-dependent mechanisms may have been responsible for the increased mortality during the early juvenile stage, and they may have acted more intensely in 1990 than in 1991 (see Fig. 3 and 4 and Table 5) considering the different numbers of juveniles harvested from the pond.

The daily growth rates in length varying from 2.5 to 2.9% in our study are comparable with those estimated for early life stages of cod (<120 d age) in other marine ponds in Norway (2.3–4.4%, Ellertsen et al. 1981; 2.4%, Øiestad et al. 1985; 2.1%, Pedersen et al. 1989). Our growth estimates are also comparable with those estimated for larval and juvenile cod (<150 d age) from some field studies (2.5% on Georges Bank, Bolz and Lough 1988; 2.3% on Browns Bank and 2.5% on Georges Bank in 1985, Campana and Hurley 1989; 2.7% in Icelandic waters, Thorisson 1989) but lower than those Economou (1987) estimated for larval and juvenile cod in the North Sea (3.5–3.9%). Our estimates of strain-specific mean daily growth rates may be biased due to differential size-selective mortality among strains. Based on our material, it was not possible to reveal the effect of size-selective mortality on growth due to long time intervals between samplings. Generally, the size distribution broadens when growth is in an accelerating phase and narrows when growth is decelerating (DeAngelis and Huston 1987). Thus the effect of size-selective mortality on strain-specific mean growth rates may be obscured by the effect of distribution of growth rates within strains, when analysing size distributions between different points of time. In our study, the instantaneous daily growth rates did not differ significantly between strains during the period from release to the juvenile phase any year, and hence were not correlated with maternal size. Monteleone and Houde (1990) found that weight-specific growth rates did not differ significantly between progeny from small and large females; however, progeny from large females grew faster in length than progeny from small females.

Different catchability of the sampling tools used for collection of cod for determination of strain frequencies and hence strain-specific growth and mortality may have influenced our results. Avoidance by larger larvae may have occurred in our samples collected with the two-chambered net during the day at the late larval stage (Morse 1989; Röpke 1989; McGurk 1992). The small differences in mean length and weight of juveniles attracted by dry feed and collected by the dip net on Days 94 and 107 in 1990 may indicate that we were sampling different size groups of the population on these days. The juveniles collected from the net pens included all size ranges of cod, and should therefore be representative for the total harvest of juveniles from the pond. In conclusion, we think that the trends in our results are fairly unequivocal in spite of different sampling methodology and thus possible differences in catchability.

Based on data from 1990, one might speculate that Strain A was inferior with respect to survival compared with Strain B, suggesting that natural selection was working on the *GPI-1** polymorphism. But the increased survival of Strain A compared with Strain B in 1991 suggests that other explanations should be considered. Jørstad et al. (1991) found that the frequency of genetically marked individuals in the reared population did not change during the period from yolk-sac larvae to mature fish 2 yr later which indicated equivalent survival potential among *GPI-1** genotypes, at least under the farming conditions used. Our results concerning growth also support the study of Jørstad et al. (1991) who found that individuals homozygous for the *GPI-1*30* allele had similar growth during the larval and juvenile stage as individuals possessing other *GPI-1** genotypes. But we estimated generally higher coefficients of variation in length data from Strain B than from Strain A. In conclusion, we found no positive indications of inferior growth and survival of genetically marked cod in the present study.

In our study, the egg size was positively related to maternal size such that smaller females tended to produce smaller eggs than larger ones. Similar tendencies have been observed by Hislop (1988), Kjesbu (1989), Zastrow et al. (1989), Monteleone and Houde (1990), and Kjesbu et al. (1992). Egg size seems to be controlled by the nutritional status, condition factor, size of mature females, final growth period before spawning, time of spawning including the temperature regime close to spawning, latitude, and number of egg batches shed (Baxter 1988; Hinckley 1990; Kjesbu et al. 1990, 1991; Buckley et al. 1991b). Although we found significant differences in length at hatching between strains both years from the regressions in Table 8, measured larval lengths at release did not differ significantly between strains (Table 4b). Hence, our data showed that larval lengths at release were less related to egg size and thus maternal size.

Knutsen and Tilseth (1985) showed that large eggs from the same spawning stock of Atlantic cod produced significantly larger larvae than small eggs. Thus, egg size might reflect maternal effects better than size of yolk-sac larvae.

Survival of a cohort tends to be positively related to growth rates during the early stages (Anderson 1988) and also seems to be positively related to body size at hatching (Rosenberg and Haugen 1982; Miller et al. 1988). A positive relationship between size of yolk-sac larvae and survival has been reported for winter flounder (*Pleuronectes americanus*, previously *Pseudopleuronectes americanus*) (Buckley et al. 1991a). In contrast, Monteleone and Houde (1990) found no significant differences in survival rates of striped bass (*Morone saxatilis*) larvae originating from large and small females. Pepin (1991) concluded that initial size did not appear to influence survival significantly in either egg, yolk-sac, or larval and early juveniles stages, although the average size per se did influence the estimated survival of larval and early juvenile fishes. However, our results indicated that the survival advantage of larger eggs did not seem to prevail until a presumed density-dependent response arose during the early juvenile stage apparently due to lack of suitable food. Hutchings (1991) showed that juvenile survival in brook trout (*Salvelinus fontinalis*) was positively related to egg size throughout the first 50 d of exogenous feeding at high and low food levels and that decreased food abundance increased mortality significantly among the smallest eggs but had a negligible effect on the largest eggs. He argued that large individuals were better competitors than small ones, and thus gained higher fitness. Trade-off between numbers and size of offspring is an important factor determining reproductive potential (Smith and Fretwell 1974; Stearns 1992), and one might expect that reducing offspring size will lead to more variable year-class strength (Hjort 1914; May 1974; Miller et al. 1988). However, recruitment variability of temperate marine fish was poorly associated with length at hatching, but the duration of the larval stage was positively correlated with recruitment variability (Pepin and Myers 1991). But our findings that small differences in body size between individuals due to maternal influence and actual age influence their survivorship through size-dependent mortality processes support the conceptual framework by Miller et al. (1988) which emphasizes the importance of initial size for survival and recruitment.

Improvements have been made in growth analysis of young fish in field studies by use of otolith microstructures (Campana and Neilson 1985; Bolz and Lough 1988; Laidig et al. 1991; Brown and Bailey 1992; Moksness 1992) and RNA–DNA ratios (Buckley and Lough 1987; Robinson and Ware 1988). However, reliable estimates of larval abundances at different ages are still difficult to obtain (Houde 1987; Taggart and Frank 1991; Bradford 1992), and thus, mortality rates may be biased. As shown by Svåsand et al. (1991), releases of genetically marked fish larvae in the sea offer the possibility of estimating growth and mortality of field-collected larvae where larval size, age, and abundance at release are known. Our study fortifies the use of genetically marked larvae as an important tool in the study of early life history of fishes.

Acknowledgements

We thank Jan P. Pedersen and John K. Stordal for assistance in collection of samples, Egil Ona for help in conducting the echo sounder surveys, and Ewa Andersen for technical assistance at the Austevoll Aquaculture Research Station. We also thank Arild Folkvord, Gunnar Nævdal, and two anonymous reviewers for their useful comments on the manuscript.

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Patterns in the Distribution and Abundance of Zebra Mussel (*Dreissena polymorpha*) in Rivers and Lakes in Relation to Substrate and Other Physicochemical Factors[1]

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Mellina, E., and J.B. Rasmussen. 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physicochemical factors. Can. J. Fish. Aquat. Sci. 51: 1024–1036.

Using SCUBA and an in situ method of quantifying substrate characteristics, we describe patterns of zebra mussel (*Dreissena polymorpha*) distribution along the St. Lawrence and Hudson rivers and in Oneida Lake, New York, and develop empirical models for their abundance. Calcium-poor waters originating from rivers draining the Canadian Shield resulted in a complete lack of zebra mussel colonization along the north shore of the St. Lawrence River east of Montreal despite an abundance of suitable substrate. Calcium concentrations of 15 mg/L or less limited the distribution of zebra mussel. The entire south shore from Cornwall, Ontario, to Île d'Orléans, Quebec, was colonized by zebra mussel wherever suitable substrate was found. Among the three systems, substrate size explained between 38 and 91% of the variability in density. Other factors such as Secchi depth, calcium concentration in the water, the presence of crayfish, native unionid abundance, and the maximum width of the river at the site increased the amount of explained variance across the different systems. A model based on substrate size also successfully explained patterns of zebra mussel abundance from published sources.

Au moyen de SCUBA et d'une méthode in situ de quantification des caractéristiques des substrats, nous décrivons les profils de distribution de la moule zébrée (*Dreissena polymorpha*) le long du Saint-Laurent et de la rivière Hudson, ainsi que dans le lac Oneida, État de New York, et nous développons des modèles empiriques de leur abondance. C'est par les eaux pauvres en calcium des cours d'eau qui drainent le bouclier canadien qu'on peut expliquer pourquoi la moule zébrée n'a pas colonisé la rive nord du Saint-Laurent à l'est de Montréal, malgré une abondance de substrats appropriés. Dans sa distribution, la moule zébrée est limitée par une concentration en calcium de 15 mg/L ou moins. L'ensemble de la rive sud, à partir de Cornwall en Ontario jusqu'à l'île d'Orléans au Québec, est colonisé par la moule zébrée sur tous les substrats qui s'y prêtent. Dans les trois réseaux étudiés, l'importance des substrats permet d'expliquer pour 38 à 91 % les variations de densité. D'autres facteurs comme la transparence au disque de Secchi, la concentration en calcium de l'eau, la présence d'écrevisses, l'abondance d'unionidés indigènes et la largeur maximale du cours d'eau à hauteur de la station, accroissent la variance expliquée d'un réseau à l'autre. Un modèle qui s'appuie sur l'importance des substrats a aussi permis d'expliquer les profils d'abondance de la moule zébrée à partir de renseignements publiés.

Received May 26, 1993
Accepted December 9, 1993
(JB948)

Reçu le 26 mai 1993
Accepté le 9 décembre 1993

The zebra mussel (*Dreissena polymorpha*) has spread rapidly since its introduction and subsequent discovery in Lake St. Clair in 1988 (Hebert et al. 1989) and is now firmly established in all the Great Lakes and in waterways along much of northeastern North America (Neary and Leach 1992; New York Sea Grant Extension 1993). Considering the mussel's potential economic and ecological impacts (Cooley 1991; Griffiths 1993), identifying factors affecting their abundance and distribution would be invaluable for the design and implementation of control programs.

To date, there are no powerful predictive models for zebra mussel abundance. Attempts at modelling have focussed on water chemistry variables as the primary predictors of zebra mussel density. Stanczykowska (1964) found no direct correlation between mussel densities and limnological variables such as pH, Secchi depth, and calcium concentrations of the water. Strayer (1991) was only able to find a weak, although significant, correlation between density and mean annual air temperature and concluded that it was not possible to predict zebra mussel abundance from published sources based on available environmental data. More recently, Ramcharan et al. (1992b) had better success in predicting zebra mussel occurrence and density using calcium, phosphate, nitrate, and pH as predictors.

Although the availability of suitable substrate is essential for the survival of postveliger zebra mussel (Stanczykowska 1977; Lewandowski 1982; Mackie et al. 1989), no published models have used substrate variables predictively. Physical factors are important determinants of zoobenthic biomass (Rasmussen 1988), and Harman (1972), Horne and McIntosh (1979), and Stern (1983) have shown qualitatively how different substrate types influence freshwater unionid abundance and distribution. A quantitative evaluation of

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[1] A contribution to the McGill University Limnology Research Center.

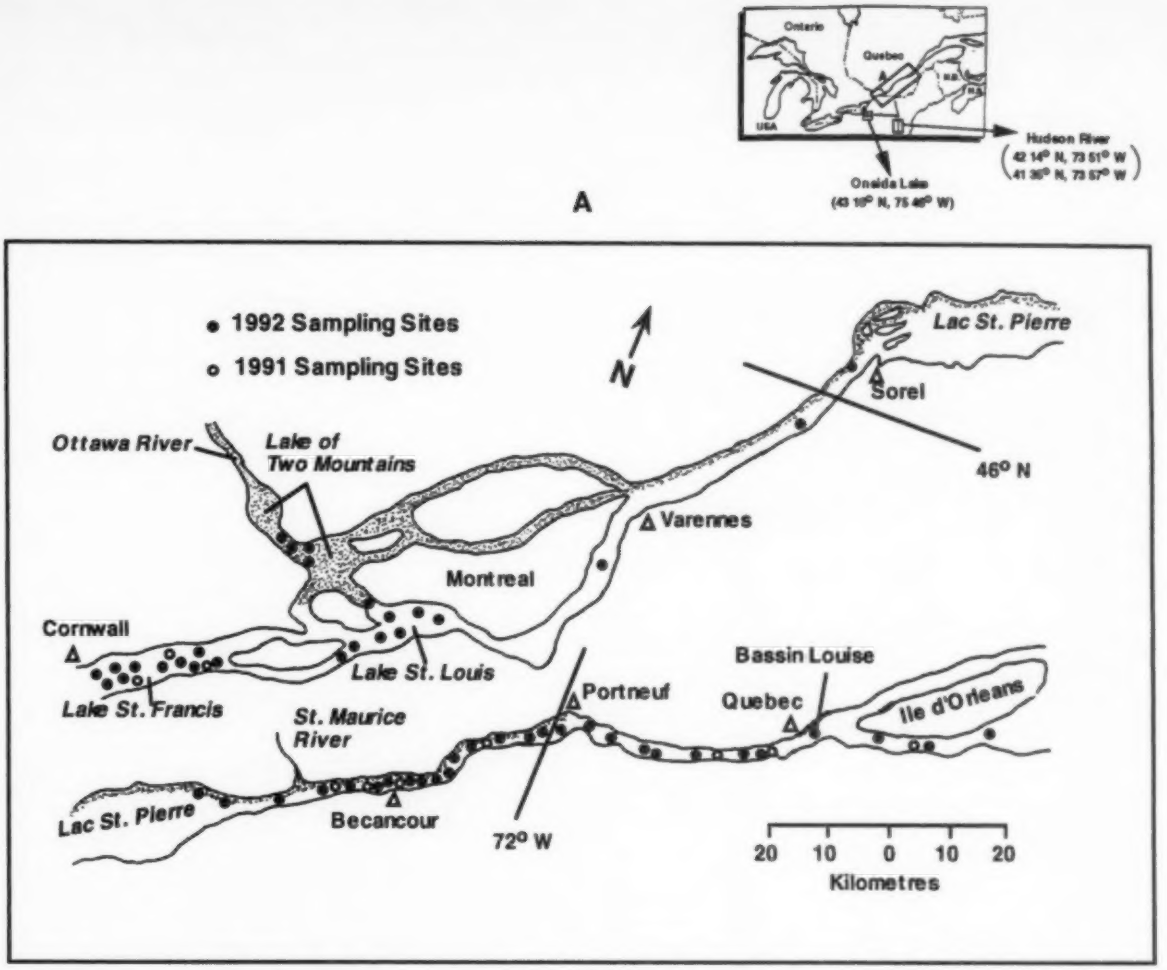
Ontario
Quebec
N.B.
N.S.
USA
Hudson River
(42 14° N, 73 51° W
41 30° N, 73 57° W)
Oneida Lake
(43 10° N, 75 45° W)
A
● 1992 Sampling Sites
○ 1991 Sampling Sites
N
Lac St. Pierre
Sorel
46° N
Ottawa River
Lake of Two Mountains
Varennes
Montreal
Cornwall
Lake St. Louis
Lake St. Francis
Bassin Louise
Portneuf
Quebec
Ile d'Orleans
St. Maurice River
Lac St. Pierre
Becancour
72° W
20 10 0 10 20
Kilometres

FIG. 1. Study areas along the St. Lawrence River. Stippled areas indicate calcium-poor waters. Approximate coordinates for the section of the Hudson River that was sampled and for Oneida Lake are shown.

substrate in combination with important water chemistry parameters may therefore improve the predictions of zebra mussel abundance models.

Zebra mussel settlement and colonization along the St. Lawrence River was expected given the potential for rapid downstream dispersal of larvae from the Great Lakes and the influence of human activities (Griffiths et al. 1991). While there have been qualitative studies on the abundance of freshwater mussels in large rivers (e.g., Wolff 1969; Thiel 1981; Miller 1988), their habitat requirements remain largely unquantified due to sampling difficulties imposed by deep, fast-flowing waters (Stern 1983; Holland-Bartels 1990). The purpose of our study was to determine the physical and chemical factors that influence zebra mussel abundance and distribution along the St. Lawrence River across a naturally occurring gradient of calcium concentration between the north and south shores. We hypothesize that along the north shore in areas draining the Canadian Shield, low calcium concentrations would make mussels rare or absent. By contrast, high calcium levels and a good supply of larvae from the Great Lakes along the south shore would probably result in the potential for a high degree of substrate-related variability in zebra mussel density. We developed an in situ method for quantitative substrate characterization that enabled us to determine the influence of substrate type on zebra mussel density and developed empirical models using linear regression analysis. We also tested the applicability of the method in the Hudson River and in Oneida Lake, New York. Finally, we tested the robustness of our models with data from literature studies that reported both zebra mussel densities as well as general descriptions of associated substrates.

Study Areas

The St. Lawrence study area comprised 57 freshwater sites along the St. Lawrence River between Cornwall, Ontario, and Île d'Orléans, Quebec, including four sites in the Lake of Two Mountains, Quebec (Fig. 1). Sampling was conducted between mid-July and the end of August 1992. An additional 11 sites were sampled in August 1991 during a preliminary study. This portion of the river was chosen for the variability in the underlying geology of the drainage basins that gave us the opportunity to study the effect of water chemistry on zebra mussel distribution. Île d'Orléans represents the limit of salt water coming from the Gulf of St. Lawrence, and tides are felt upstream until Lac St. Pierre (Couillard 1982).

Almost the entire water mass along the St. Lawrence River between Cornwall and Montreal originates from the Great Lakes and is characterized by a greenish hue and relatively high calcium concentrations (Lamarche et al. 1982; Vincent et al. 1991). Along this section of the river the drainage basin is composed primarily of calcareous sedimentary rock (Clark and Stearn 1968; Bobée et al. 1981). East of Montreal the existence of different hydrological corridors results in a distinct calcium gradient between the two shores of the river. Water along the south shore with its underlying calcareous geology is fed by the Great Lakes and continues to contain high calcium concentrations. Along the north shore, however, the main sources of water are the Ottawa and St. Maurice rivers, both of which drain parts of the erosion-resistant Canadian Shield (Frenette and Verrette 1976; Lamarche et al. 1982). The result is a thin band of brownish, calcium-poor water running along the north shore of the St. Lawrence River (east of the point of confluence with the Ottawa River) joined to a large band of green, calcium-rich water along the south shore originating from the Great Lakes (Lamarche et al. 1982; Vincent et al. 1991). This distinct calcium gradient remains stable until the vicinity of Portneuf (Fig. 1), where the tidal influence is sufficient to ensure complete mixing of the water mass, thereby obliterating the water chemistry gradient (Couillard 1982).

Sites along the St. Lawrence River were chosen using navigational charts published by the Department of Fisheries and Oceans which give approximate substrate compositions. Between Montreal and Lac St. Pierre the riverbed is primarily sandy and was therefore sampled less intensively than the rest of the river. Sites were also chosen to maximize the variability in calcium, depth, and Secchi visibility. In addition to natural substrates, two sites were chosen along the river representing artificial structures: the walls (1) at the port of Becancour, Quebec, and (2) within Bassin Louise, Quebec, which is a completely enclosed basin with access to the main river limited by locks and protected from some of the physical factors affecting the rest of the river (i.e., wind, waves, and current).

Sampling was also conducted at 11 sites along a freshwater tidal section of the Hudson River from Catskill to New Hamburg during the first week of July and at five sites in the hardwater, moderately eutrophic Oneida Lake in upper New York State during mid-June 1992 (Fig. 1). These two systems were investigated to assess whether zebra mussel distribution in relation to substrate was similar across different systems and to test the applicability of our method of quantifying substrates in a second river system and in a lake. In addition, these two systems were also characterized by early stages of zebra mussel colonization making them ideal for comparisons with the St. Lawrence River.

Methods

Sampling Techniques

SCUBA diving was employed at all sites to determine zebra mussel densities. Under certain conditions, SCUBA gives more accurate estimates of density than bottom samplers (Wisniewski 1974; Stanczykowska 1977) and also allows for substrate observations (Stern 1983). In addition, the close proximity of the diver to the substrate meant that zebra mussel as small as 2–3 mm in length were clearly discernible.

A 1-m^2 aluminum quadrat was randomly placed on the river/lake bottom and all visible zebra mussel within it were counted in situ. Due to safety problems encountered with fast currents along the St. Lawrence River, subsequent quadrats within a site could only be placed by blindly throwing the quadrat away from the diver (thus minimizing bias) and repeating counts. While this sampling protocol was not strictly random, biases have further been reduced by averaging estimates over each site when performing the analyses. Because the diver attempted to count approximately 100 mussels for each quadrat (this being the optimum number based on experience to preserve reliability, efficiency, and safety), quadrat sizes varied from 0.01 to 1 m^2 and the number of quadrats counted at each site varied accordingly (from 3 to 20). The quadrat was adjustable so that smaller areas could be counted when mussel densities exceeded approximately 100/m^2. The size and number of replicate quadrats counted within a site were determined according to Downing and Downing (1992), who predicted that with a density of 100 mussels/m^2, two replicate 1-m^2 quadrats were required to obtain a precision of 20%. Replicate quadrats were counted at each site where zebra mussel were present with the exception of five sites in the St. Lawrence where only one quadrat per site was counted due to difficulties encountered with fast currents. An underwater light was used to aid in the detection of mussels in areas of low visibility. Size distributions and biomass of zebra mussel were not recorded due to fast currents which did not allow us time to remove all the mussels from the substrate. However, biomass of zebra mussel is usually related to density within a given water body (Stanczykowsa 1976).

In situ counting proved the most efficient method for estimating zebra mussel density, enabling the diver to descend to the river/lake bottom unencumbered with collecting bags and allowing for a greater number of quadrats to be counted. The accuracy of the in situ density estimates was tested by removing zebra mussel from within 10 quadrats and bringing them to the surface for counting. These counts were then compared with the in situ counts for the same quadrats. Differences between the two methods did not exceed 5%. Densities from test counts ranged from approximately 10 to 150 mussels/quadrat, which was within the range of mussels counted in each quadrat during sampling.

Substrate composition was also determined in situ by measuring the lengths of the different rocks within a quadrat and then visually estimating the percent areal coverage of each type of substrate of a given size (e.g., a quadrat could be covered by 25% sand, 25% gravel of 3-cm diameter, and 50% boulders of 30-cm diameter). The different substrate types were converted to the phi scale (ϕ) by transforming them to the negative log base 2 of the particle size in millimetres (Hakanson and Jansson 1983). Each substrate's phi value was multiplied by its percent contribution to the total coverage and then summed to give a mean weighted particle size (henceforth referred to as substrate size) for each quadrat. The more negative the substrate size, the larger the particle. Thus, for each quadrat, we obtained an estimate

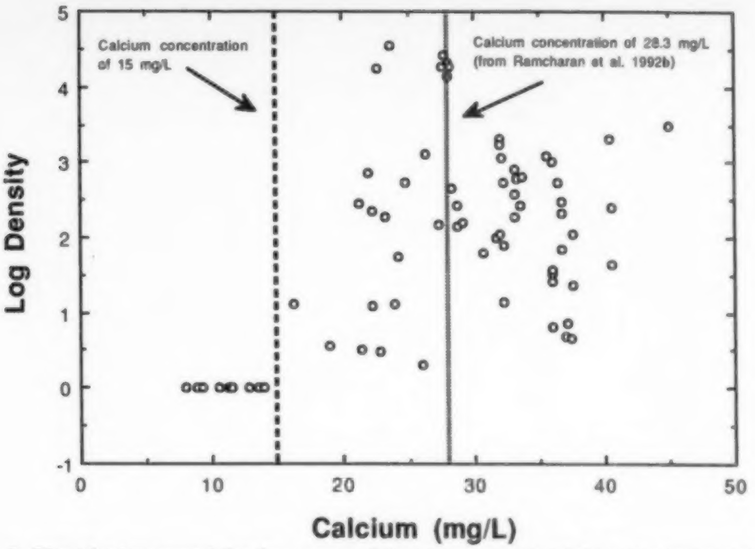

FIG. 2. Plot of zebra mussel density versus calcium concentration of the water (averaged over each site) for the combined data set including all three systems. Only those density estimates associated with suitable substrate sizes (with phi values less than 2) were chosen to remove the effects of unsuitable substrate on mussel density. The threshold concentrations suggested by this study and by Ramcharan et al. (1992b) are shown.

of zebra mussel density (which included all zebra mussel counted within a quadrat) and an associated measure of substrate size. Artificial walls were dealt with by assuming they represented a particle with a length of 1 m and were assigned a phi value of −9.967 (100% cover with a 1000-mm particle). Sampling methods remained constant across the three systems (the St. Lawrence and Hudson rivers and Oneida Lake) and all measurements were made by the same diver so as to minimize bias when assessing mussel density and substrate size.

The presence or absence of crayfish was determined by uncovering rocks around an area of approximately 100 m^2 at each site and was accounted for in the regression models with a dummy variable. Native unionid abundance was estimated semiquantitatively by grouping them into three categories based on their areal coverage within a quadrat, low (0–25%), medium (26–50%), and high (>50%), and was accounted for in the multiple regression models with a dummy variable. Only their abundances (and not their contributions as a substrate) were considered in the models. Because sites along the St. Lawrence River downstream from Lac St. Pierre, Quebec, as well as sites along the Hudson River experience daily fluctuations in water levels due to tides, all depth estimates were taken from navigational charts on which depths were reduced to Lower Low Water (Canadian Tidal Datum). The maximum width of the river as well as the distance from site to shore at each site was also measured from these charts. Sites within Bassin Louise were included in the multiple regressions for the St. Lawrence River and were accounted for with a separate lentic/lotic dummy variable due to their isolation from the main river channel.

A water sample was taken at each site in clean, plastic bottles and refrigerated for future analysis. In the laboratory, samples were analyzed for water chemistry according to the following methods modified from Clesceri et al. (1989) by Hach, Inc. for use on a Hach portable colorimeter: calcium (titration using CalVer® indicator), true and apparent color (platinum–cobalt colorimetric method), and total phosphorus (TP) (ascorbic acid method according to Griesbach and Peters 1991).

Linear Regression Analysis

All statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1989). Any variable spanning more than 1 order of magnitude was log base 10 transformed, while zebra mussel densities were $\log_{10}(X+1)$ transformed to reduce undue influences of large values and to stabilize the variance of the dependent variable (Kleinbaum et al. 1988). In addition, estimates of all the variables were averaged over each site before performing the analyses. We searched for statistical relationships between zebra mussel density and the physical and chemical variables gathered at each site. Significant differences in calcium levels between shores along the St. Lawrence River led us to analyze the entire data set for the St. Lawrence using two approaches: (1) by grouping the variables a posteriori according to shore (to remove the effect of substrate size on density along the calcium-poor north shore) and (2) by analyzing the entire data set irrespective of shore.

Linear regression analysis was first attempted between mussel density and our quantitative characterization of substrate for each system separately to determine the amount of variability in density that could be explained using substrate size alone. Multiple regressions were run using the entire data set for each system to generate the most powerful predictive models. Regression diagnostics analysis (including residual analysis, normal probability plots, and tests for multicollinearity between predictors) were run for all the regression models to ensure the appropriateness of a linear

TABLE 1. Averaged physical and chemical characteristics of sites along the St. Lawrence and Hudson rivers and Oneida Lake. SE is standard error; *n* is the number of sites.

	Density (no./m^2)	Substrate	Temperature (°C)	Depth (m)	Secchi (m)	Max. width of river at site (km)	Distance from site to shore (km)	pH	Conductivity (µS/cm)	Calcium (mg/L)	TP (µg/L)	Apparent color (Pt–Co units)
St. Lawrence north shore (east of Montreal and the Lake of Two Mountains)												
Max.	0.00	1.58	21.40	4.60	2.00	5.50	2.00	9.70	223.00	14.00	83.33	541.00
Min.	0.00	−9.97	8.10	0.50	0.20	2.00	0.10	6.29	50.00	8.00	12.84	48.00
Mean	0.00	−4.89	15.56	2.18	1.04	3.45	0.64	7.38	114.30	10.89	29.47	109
SE	0.00	1.15	1.62	0.35	0.15	0.30	0.19	0.31	15.35	0.61	6.27	43.77
n	11	11	11	11	11	11	11	11	11	11	11	11
St. Lawrence south shore												
Max.	26883	3.72	21.20	11.00	5.25	14.50	3.00	8.60	666.00	37.60	46.40	88.00
Min.	0	−9.97	16.30	1.80	0.50	0.50	0.10	7.25	140.00	16.20	4.57	6.00
Mean	2444	−3.64	19.27	4.01	2.07	4.14	1.00	7.90	267.95	31.82	20.38	25.05
SE	925	0.51	0.22	0.31	0.16	0.36	0.11	0.05	10.74	0.77	1.25	2.62
n	46	46	46	46	46	46	46	46	46	46	46	46
Hudson River												
Max.	37500	6.14	24.30	8.84	1.20	1.40	0.56	7.19	214.00	26.40	140.36	101.50
Min.	0	−9.97	23.00	1.82	0.40	0.68	0.04	6.83	183.00	22.00	28.50	29.00
Mean	5091	−2.97	23.38	2.96	0.96	1.10	0.28	7.10	199.38	23.96	67.68	48.27
SE	3440	1.95	0.14	0.60	0.06	0.07	0.06	0.03	3.76	0.41	10.46	6.14
n	11	11	11	11	11	11	11	11	11	11	11	11
Oneida Lake												
Max.	3161	5.86	21.80	6.71	3.50	n/a	2.96	8.20	336.00	45.00	44.71	70.00
Min.	42	−4.83	19.40	3.05	2.50		0.28	7.99	298.00	22.20	3.50	17.33
Mean	1155	−0.55	20.54	4.05	2.90		1.33	8.14	311.80	37.76	14.51	30.57
SE	624	1.96	0.41	0.71	0.19		0.45	0.04	6.38	3.99	7.28	9.91
n	5	5	5	5	5		5	5	5	5	5	5

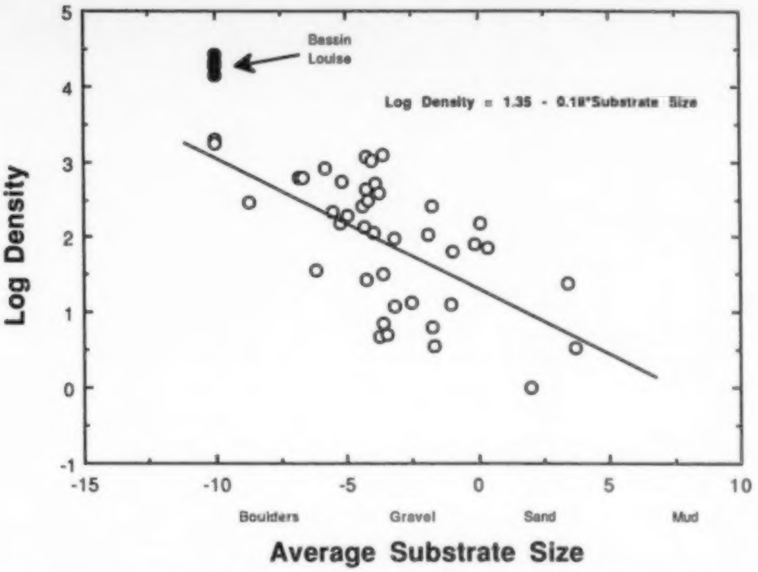

FIG. 3. Relationship between zebra mussel density and substrate size (the mean weighted phi value for each quadrat averaged over each site) for south shore sites along the St. Lawrence River ($R^2 = 0.38$, $p < 0.001$, $n = 41$). Densities from Bassin Louise are not included in the regression.

model, that the assumptions underlying the models were not violated, and that spurious correlations were not generated (Kleinbaum et al. 1988).

The extent (if any) of the increase in zebra mussel abundance along the St. Lawrence River between 1991 and 1992 was also determined using density and substrate size estimates (gathered using similar protocols) from the 11 additional sites sampled in 1991 (Fig. 1). These density estimates were compared, using an ANCOVA, with estimates from 11 sites in the present study that had comparable substrate size values. The regression coefficient for the year factor was used as an estimate of the average increase in density along the river between the two years.

Literature Studies

To test the robustness of our method of quantifying substrate and to support the importance of substrate size in determining zebra mussel density, a composite model was formed relating density to substrate size using the data gathered in Oneida Lake and along the Hudson River and the south shore of the St. Lawrence River. The model included a categorical variable to distinguish between lakes and rivers and also included Bassin Louise (which was classified as a lake given the protected nature of the enclosure). The predictions of this composite model were then tested with a literature data set compiled from mostly European studies of lakes and rivers that jointly reported a general description of substrate type and zebra mussel abundance. The literature studies were chosen regardless of the methods used to gather density estimates. A total of 38 studies were found, including five recent studies of zebra mussel in the Great Lakes and a preliminary study carried out in the Great Lakes in 1991 by ourselves that yielded six additional sites. These six sites were not combined with the sampling data set, since quantitative density estimates were coupled to qualitative substrate descriptions.

Substrate descriptions were converted to the phi scale according to Hakanson and Jansson (1983) and to the Wentworth classification as follows: mud/clay = 9, silt = 6.5, sand = 2, gravel = −3.5, and boulders = −8. Stones were arbitrarily assigned a length of 10 cm and a phi value of −6.644. Where densities were reported for hydrotechnical installations, it was assumed that these were taken from walls and were therefore assigned a phi value of −9.967 as the corresponding substrate size. Some studies (e.g., Lundbeck 1926; Stankovic 1951) reported mussel densities on a bed of empty shells (a "shell zone"). In these cases the substrate was assumed to be completely covered with shells averaging 2 cm in length and was assigned a phi value of −4.322 (100% cover with 2-cm shells).

When a combination of different substrates was reported, their respective contributions to the weighted phi value were equally divided. For example, if sand and gravel were reported as the substrate for a particular site, then 50% of the final phi value was composed of sand and 50% was composed of gravel. Whenever a study reported different mussel densities for a particular substrate type, the densities were averaged for that substrate within the study. Sites with macrophytes were avoided, since macrophytes were rare in the present study and were not accounted for in the models.

Results

St. Lawrence River

When the calcium and density data were pooled for all three systems, there appeared to be a calcium threshold level of 15 mg/L below which no zebra mussel were found (Fig. 2). For the St. Lawrence River, with its natural calcium gradient between the north and south shores, sites were classified according to shore based on this calcium threshold level of 15 mg/L. Calcium levels in the water were different between shores (t-test, $p < 0.001$) and ranged

TABLE 2. Multiple regression models obtained for zebra mussel density for the St. Lawrence and Hudson rivers, Oneida Lake, and the literature studies. Numbers in parentheses following predictors are SE of the coefficients. Significance: $^{*}p < 0.05$, $^{**}p < 0.005$, $^{***}p < 0.001$.

Equation	r^2	SE	n
St. Lawrence River (south shore)			
(1) $\log \text{density} = 0.05 - 0.13\ \text{substrate}\ (0.03)^{***} - 1.86\ \log \text{Secchi}\ (0.39)^{***}$ $+ 0.05\ \text{calcium}\ (0.05)^{**} + 0.69\ \text{clams}\ (0.13)^{***} - 0.41\ \text{crayfish}\ (0.16)^{*}$ $+ 2.21\ \text{lentic site}\ (0.32)^{***}$	0.83	0.45	46
St. Lawrence (north and south shores)			
(2) $\log \text{density} = -1.67 - 0.09\ \text{substrate}\ (0.02)^{***} - 1.79\ \log \text{Secchi}\ (0.38)^{***}$ $+ 0.11\ \text{calcium}\ (0.01)^{***} + 0.52\ \text{clams}\ (0.13)^{***} + 2.78\ \text{lentic site}\ (0.33)^{***}$	0.82	0.56	57
Hudson River			
(3) $\log \text{density} = -3.35 - 0.30\ \text{substrate}\ (0.03)^{***}$ $+ 4.20\ \text{max. width of river}\ (0.96)^{**}$	0.89	0.51	11
Oneida Lake			
(4) $\log \text{density} = 1.70 - 0.17\ \text{substrate}\ (0.003)^{***} + 0.02\ \text{calcium}\ (0.001)^{**}$	0.99	0.02	5
Composite model (St. Lawrence south shore, Hudson, Oneida)			
(5) $\log \text{density} = 1.38 - 0.19\ \text{substrate}\ (0.02)^{***} + 1.14\ \text{lake}\ (0.23)^{***}$	0.67	0.66	62
Literature studies (lakes)			
(6) $\log \text{density} = 2.34 - 0.23\ \text{substrate}\ (0.02)^{***}$	0.75	0.82	72
Literature studies (rivers)			
(7) $\log \text{density} = 1.43 - 0.14\ \text{substrate}\ (0.05)^{***}$	0.29	1.05	18

from 8 to 14 mg/L for the north shore of the St. Lawrence and from 16 to 38 mg/L for the south shore (Table 1).

The north shore (Montreal to Portneuf) was devoid of zebra mussel despite an abundance of large rocks, while the entire south shore (Cornwall to Île d'Orléans) was colonized wherever suitable substrate (defined as having a phi value less than 2, which corresponds to 100% sand) was found (Table 1). We did not find settled zebra mussel directly on sand or on smaller grain sizes. At sites where the substrate was composed of sand or silt, native unionids often provided the only available hard substrate. The highest zebra mussel densities were found in Bassin Louise, at the port of Becancour, and off the island of Montreal. In general, densities were higher on artificial substrates than on natural substrates. No settled zebra mussel were found in the Lake of Two Mountains. In addition, the comparison between densities at the 11 sites from 1991 with comparable sites from this study revealed an average sixfold increase in zebra mussel abundance along the St. Lawrence River between 1991 and 1992.

Using linear regression, average substrate size by itself was able to explain 38% of the variability in zebra mussel density for south shore sites (Fig. 3). In the protected site of Bassin Louise, densities were over an order of magnitude higher than in the main river channel (Fig. 3). The best overall abundance model for the south shore ($r^2 = 0.83$) had zebra mussel density negatively correlated with substrate size, Secchi depth, and the presence of crayfish and positively correlated with the categorical classification of unionid abundance, with the lotic/lentic dummy variable, and with calcium concentrations in the water (Table 2). The addition of north shore sites (those below the calcium threshold) resulted in a slight decrease in the predictive power of the multiple regression model, and the presence of crayfish no longer became a significant predictor at the 0.05 level (Table 2). Sampling was not biased by the date on which it took place, as calendar day was an insignificant predictor in the model. There was no multicollinearity between predictors and none of the assumptions underlying linear regression models (Kleinbaum et al. 1988) was violated.

Hudson River and Oneida Lake

When the density and substrate size data were combined across all three systems, mussel densities in the Hudson were comparable with those found in the St. Lawrence, while densities in Oneida Lake were generally an order of magnitude higher given the same substrate size values (Fig. 4). In the Hudson River, substrate size as a predictor was able to account for 67% of the variability in zebra mussel density (Fig. 4). The best multiple regression model for the Hudson ($r^2 = 0.89$) had zebra mussel density negatively correlated with substrate size and positively correlated with the maximum width of the river at the site (Table 2).

In Oneida Lake, substrate size accounted for 91% of the variability in zebra mussel density (Fig. 4). Adding calcium concentrations of the water as a predictor in a multiple

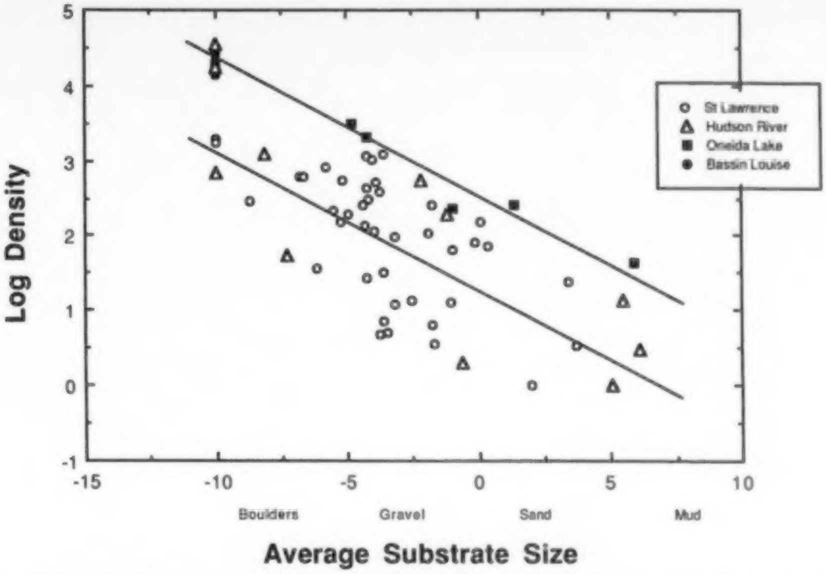

FIG. 4. Relationship between zebra mussel density and substrate size averaged over each site for the three systems combined. The regression equations for the Hudson River and Oneida Lake, respectively, are (1) log density = 1.53 − 0.20·substrate size ($R^2 = 0.67$, $p < 0.001$, $n = 11$) and (2) log density = 2.55 − 0.17·substrate size ($R^2 = 0.91$, $p < 0.001$, $n = 5$).

TABLE 3. Comparison of predictors and their influence on zebra mussel density in the models for the St. Lawrence and Hudson rivers and Oneida Lake.

St. Lawrence River (all sites)	*p* value	Hudson River	*p* value	Oneida Lake	*p* value
Substrate (phi) (−)	<0.001	Substrate (phi) (−)	<0.001	Substrate (phi) (−)	<0.001
log Secchi (−)	<0.001	Max. width of river (+)	0.002	Calcium (+)	0.003
Calcium (+)	<0.001				
Clams (+)	<0.001				
Crayfish (−) (south shore only)	0.01				
Lentic site (+)	<0.001				

regression explained a further 8% of the variability (Table 2). Oneida Lake also had the highest calcium concentrations of all three systems (ANOVA, $p < 0.001$).

The slopes of the regressions of density against substrate size were similar in all three systems (*t*-tests, $p > 0.15$; Fig. 4). However, while the intercepts of the St. Lawrence and Hudson River regressions were also similar to each other (*t*-test, $p > 0.30$), the intercept for the Oneida Lake regression was higher than those of the two river systems (*t*-test, $p < 0.001$). The St. Lawrence sites that were judged to be lentic (Bassin Louise) fell along the Oneida Lake regression line. Substrate size accounted for the greatest proportion of variability in zebra mussel density in the models and was the common thread across the three systems (Table 3).

Literature Studies

The composite model explained 67% of the variability in zebra mussel density from the three systems we investigated (Table 2). In testing this model, the literature lake densities tended to fall above those predicted by the lake regression (Fig. 5). This is particularly evident for the North American lakes. The river densities, on the other hand, tended to be scattered on either side of the predicted river regression (Fig. 5). In a model generated from the literature data, substrate size explained 75% of the variability in zebra mussel density for the 72 lake sites and 29% of the variability in density for the 18 river sites (Table 2).

Discussion

Suitable water chemistry seems primarily to set the threshold for the presence of zebra mussels rather than determine their abundance, and calcium levels along the north shore of the St. Lawrence River may be the limiting factor affecting their distribution within the river. Sprung (1987) observed limited survival of zebra mussel larvae at calcium concentrations of 12 mg/L, while Vinogradov et al. (1993) found waters with calcium concentrations below 10–12 mg/L to be unsuitable for normal zebra mussel calcium metabolism. The minimum calcium requirement for survival and growth of adult zebra mussel was found to be between 3 and 8 mg/L

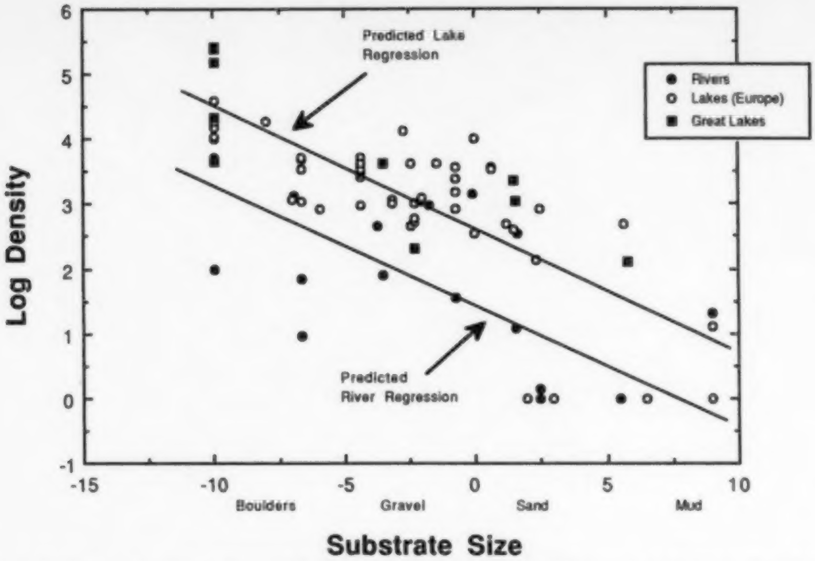

FIG. 5. Test of the predictions of the composite model (formed by pooling the sampling data from all three systems) using literature data. The solid lines represent the predicted regressions for rivers and lakes according to model 5 in Table 2. Literature references comprise the following. *(1) Rivers:* Behning 1928 (River Volga); Berg 1948 (River Susaa); Kachalova and Sloka 1964 (Daugava River); Kovalak et al. 1993 (Detroit River); Smit et al. 1993 (River Ijssel); Wielgosz 1979 (River Lyna); Wielgosz 1981 (River Wel); Zhadin and Gerd 1961 (River Volga). *(2) European Lakes:* Berg 1938 (Lake Esrom); Bianchi et al. 1974 (Lake Garda); Biryukoi et al. 1964 (Babiinski backwater); Dall et al. 1984 (Lake Esrom); Dusoge 1966 (Lake Mikolajskie); Ehrenberg 1957 (Grosser Ploner See, Kleiner Ploner See, Trammer See); Gizinski and Toczek-Boruchowa 1972 (Goplo Lake); Gizinski and Kadulski 1972 (Goplo Lake); Jonasson 1978 (Lake Esrom); Kachanova 1962 (Uchinsk Reservoir, cited in Morton 1969b); Kajak and Dusoge 1976 (Lake Sniardwy); Kornobis 1977 (unspecified, one of the Konin lakes); Lewandowski 1991 (Lake Kolowin); Lewandowski and Stanczykowska 1986 (Lake Zarnowieckie); Lundbeck 1926 (Suhrer See, Trammer See, Ploner See, Becken See, Schaal See); Michalkiewicz 1991 (Rosnowskie Duze Lake); Mikulski and Gizinski 1961 (Wdzydze Lake); Pieczynska 1972 (Lake Mikolajskie); Sapkarev 1975 (Lake Doiran); Shevtsova and Kharchenko 1981 (N. Crimean canal); Stanczykowska 1977 (Lake Konin); Stankovic 1951 (Lake Doiran); Walz 1973 (Lake Constance); Wisniewski 1990 (Lake Druzno, Wloclawek Dam); Wisniewski 1974 (Goplo Lake); Wundsch 1924 (Muggel See); Zhadin and Gerd 1961 (Sartlan Lake). *(3) Great Lakes*: Dermott et al. 1993 (Lake Erie); Hebert et al. 1989, 1991 (Lake St. Clair); Kovalak et al. 1993 (Lake Erie); Leach 1993 (Lake Erie); our 1991 study (Lake Erie, Lake St. Clair).

but in the order of 13 mg/L for veligers (S. Hincks and G.L. Mackie, University of Guelph, Guelph, Ont., personal communication). These results support the findings of the present study of a calcium threshold of 15 mg/L limiting zebra mussel distribution along the St. Lawrence River.

Neary and Leach (1992) stressed the need to account for the natural temporal variability in calcium concentrations when trying to determine threshold levels. The calcium threshold value of 28.3 mg/L reported by Ramcharan et al. (1992b) may be an overestimation given the presence of zebra mussel along the south shore of the St. Lawrence River at sites with calcium concentrations of 16 mg/L (Table 1). However, our calcium estimates are derived from single samples, while the data from Ramcharan et al. (1992b) were averaged over longer periods. To test whether or not our estimates are representative of mean values, we turned to published studies that report calcium data for the St. Lawrence River averaged over longer time periods. Vincent et al. (1991) found mean calcium concentrations (averaged over a period between May and August 1982) of 17 mg/L for a north shore site and 48 mg/L for a south shore site situated near Becancour, Quebec. Similarly, Couillard (1982) found mean calcium concentrations of 12 mg/L for north shore sites and 47 mg/L for south shore sites covering a period of 5 mo, and Vincent (1981) reported a mean calcium concentration of 29 mg/L averaged over a year for a south shore site situated 40 km east of Lac St. Pierre, an area in which we found adult zebra mussel. Further support for the validity of our threshold level of 15 mg/L can be found if one considers that marked seasonal fluctuations in calcium levels usually occur in hardwater systems, while calcium levels in softwater systems (typically below saturation levels) exhibit only minor seasonal variations (Wetzel 1983). Given that the amount of dissolved calcium in a water body depends on many other factors (such as temperature and pH), we can only apply our threshold level of 15 mg/L with confidence to the St. Lawrence River. Future studies may investigate the generality of this threshold by seeing whether softwater lakes draining the Canadian Shield are successfully colonized by zebra mussel.

While calcium may limit zebra mussel distribution, it is in itself a poor predictor of abundance. In the density models for the St. Lawrence River and Oneida Lake (Table 2), calcium was a significant predictor but only explained a small portion of the variability in mussel density. In addition, Ramcharan et al. (1992b) had greater success in predicting zebra mussel occurrence (presence/absence) than density using pH and calcium as predictors, although in their study the data were averaged for different water bodies, while ours were averaged over different sites.

Within sites with suitable water chemistry, the survival of zebra mussel is dependent on their finding suitable substrates (Stanczykowska 1977; Lewandowski 1982). The majority of variability in zebra mussel density along the St. Lawrence and Hudson rivers and in Oneida Lake was accounted for by substrate size (Fig. 3 and 4), supporting the idea that physical factors play a more important role in determining local abundance than water chemistry variables (Neary and Leach 1992). In addition, although mussel densities in each system were affected by different factors (Table 3), substrate size remained the dominant factor across the three systems. Even in the absence of these detailed data, a conversion of gross substrate descriptions to the phi scale showed substrate size to be an important determinant of mussel density in the literature data set (Table 2; Fig. 5).

The contribution of substrate size to explaining variability in density varied between systems, explaining a greater portion in lake models than in river models (Table 2; Fig. 4). While this may simply be an artifact of disparate sample sizes, it may also reflect some fundamental differences between rivers and lakes. Zebra mussel densities are usually lower in rivers than in lakes (Stanczykowska 1977), and in comparing our three systems, densities in Oneida Lake were generally 1 order of magnitude higher than in either river system given the same substrate size values (Fig. 4). If densities in lakes are governed primarily by substrate size (as shown by the Oneida Lake model), then mussel populations in rivers may be affected by other factors such as the effects of current on larval settlement and the possible dilution of larval densities due to rapid flushing in rivers. These effects may be manifested indirectly in lowered adult densities in rivers when compared with lakes.

Other physical variables that potentially affect sediment particle size such as slope and exposure (Rowan et al. 1992) were not of significant value in our models, possibly due to the narrow range of these values and the overriding importance of substrate size. Exposure, however, was highly correlated ($r = 0.74$) with substrate size in the Oneida Lake data set and may prove useful as a surrogate variable for substrate in future studies. Macrophytes, although absent at our sites, can provide important substrates for larval settlement (Lewandowski 1982) and will need to be included in future general models of zebra mussel abundance.

The scatter around the density – substrate size models may be further reduced by refining our method of quantifying substrate. Mussel densities were only determined within a projected metre square boundary which did not take into account real surface area available for colonization. The precision of the models may therefore be improved by including a measure of surface area in addition to the conversion to phi. To further reduce bias and improve the accuracy of the assessment of percent areal cover by different substrates, a photograph can be taken of the quadrat on the river or lake bottom (Bohnsack 1979; Foster et al. 1991). The photograph can then be scanned with the aid of a computer and the percent cover of each substrate type determined more accurately, possibly increasing the predictive power of models and reducing between-diver bias.

The negative correlation between zebra mussel abundance and Secchi depth in our model (Table 2) may reflect a preference for dark areas in the St. Lawrence River. Postveliger zebra mussel exhibit negative phototaxis in that they preferentially colonize the undersides and crevices of different substrates (Morton 1969a), although this preference may also be linked to the avoidance of predators, water turbulence, and current and ice scour (Yankovich and Haffner 1993). Secchi depth was colinear with TP, and if TP can be considered a measure of productivity in rivers, then the correlation between Secchi and abundance may indicate a positive association between abundance and productivity. Ramcharan et al. (1992b) found phosphorus concentrations to be negatively correlated with zebra mussel density, although the increased range in their TP values relative to ours may account for this difference. Stanczykowska (1984) suggested that nutrient levels may only adversely affect abundance at high concentrations, and the difference in the range of values may account for the difference in trends observed between their model and ours.

Unionid abundance was also an important factor in determining zebra mussel abundance in the St. Lawrence River. When presented with a choice of different substrates on which to settle, Lewandowski (1976) found native unionids to be preferred by zebra mussel. On soft substrates (e.g., mud, sand), unionids often provide the only hard substrate for initial mussel colonization (Lewandowski 1976; Hebert et al. 1991; Hunter and Bailey 1992). Unionids were heavily colonized in the Hudson River and in Oneida Lake, but were not significant predictors in the models representing these systems. The importance of hard substrate availability may also decrease over time as zebra mussel begin colonizing soft substrates by forming mats extending from an initial point of colonization such as on native unionids or on dead zebra mussel shells (Morton 1969b; Lewandowski 1982; Ramcharan et al. 1992b).

Although crayfish are unlikely to control whole zebra mussel populations, they may limit local densities and size distributions (H.J. MacIsaac, University of Windsor, Windsor, Ont., personal communication). The negative correlation between mussel density and the presence of crayfish in the St. Lawrence River (Table 2) may be an indication of the potential impact crayfish can exert on mussel densities. Predation of zebra mussel by crayfish has also been shown by Piesek (1974) and Love and Savino (1993). Blue crab (*Callinectes sapidus*) may have a similar effect on local densities of zebra mussel in the Hudson River where the two ranges overlap (Strayer et al. 1993), and although crabs were noticed during sampling in the Hudson, they were not sampled rigorously and therefore not included in the analyses.

Based on 16 European studies, Strayer (1991) found zebra mussel abundance to be related to stream size in running waters, with mussels rarely occurring in streams less than 30 m wide. A similar pattern appeared in the Hudson River, where the maximum width of the river at the site was positively correlated with mussel density (Table 2). However, as Strayer (1991) pointed out, no ecological mechanisms are known to explain this pattern.

In certain European lakes, zebra mussel populations have fluctuated dramatically (Stanczykowska and Lewandowski 1993), and the temporal variability in densities must be addressed before any predictive model can be successfully used. While the present study sheds little direct light on this aspect, we might expect North American zebra mussel populations to continue increasing relative to European populations; examination of the literature model with respect to this question suggests that densities in Oneida Lake are likely to continue to increase, while the river populations may be closer to an equilibrium level (Fig. 5). Alternatively, some authors have suggested that populations may overshoot equilibrium levels only to crash to more stable levels as a result of food or of some other resource limitation (Cooley 1991; O'Neill and MacNeill 1991; MacIsaac et al. 1992), but the evidence for this is tenuous. Population fluctuations would also be more difficult to model, although attempts in this direction have been made (Ramcharan et al. 1992a).

There is evidence for increases in zebra mussel populations between 1991 and 1992 within the three systems we investigated. During this period the population along the Hudson River increased by 100–1000 times (Strayer et al. 1993), while in Oneida Lake, densities have increased approximately 30-fold from June to October 1992 (E. Mills, Cornell University, New York, N.Y., personal communication). Along the St. Lawrence River the increase has been less dramatic, with densities increasing sixfold on average. Further monitoring may help to establish the extent of future population increases in these three systems and may also help determine whether or not the river populations are approaching equilibrium compared with Oneida Lake.

In summary, we linked zebra mussel abundance to a variety of physical and chemical variables in rivers and lakes. Water chemistry appears to set a threshold level for the presence of zebra mussel, and once waters are chemically suited to support zebra mussel physiological processes, physical factors (in particular, substrate size) tend to limit their local abundance. Our sediment evaluation method allows for a quick visual assessment of the substrate and a simple mathematical conversion. This method also allows for density comparisons to be made between different sites or across different systems by factoring in effects of substrate. In addition, this study reinforces the need for site-specific data given the local nature of zebra mussel settlement and colonization. Predictive models such as these in conjunction with maps forecasting the potential spread of zebra mussels will be highly effective in aiding control and monitoring programs by pinpointing areas most likely to be invaded and allowing for an assessment of the degree of infestation.

Acknowledgements

We thank B. Sander, S. Kesting, J. Tambasco, M. Favasoli, M. DiCapua, and J. Hepworth for their field assistance and vigilance while sampling. We also thank R. Lehmann and T. Herra for translating relevant German and Polish literature and two anonymous reviewers for helpful comments on earlier versions of this manuscript. E.M. is especially grateful to Dr. Ed Mills and Ed Roseman of Cornell University and to Dr. Dave Strayer of the Institute of Ecosystem Studies for their invaluable help and encouragement at Oneida Lake and on the Hudson River and to Bettina Sander and Stephan Kesting for their support throughout the study. We also acknowledge the support and encouragement of L. Lapierre and B. Cusson of Centre St. Laurent (Environment Canada). This work was supported by grants from NSERC to J.B.R. and an FCAR scholarship to E.M.

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Effects of the Bacterial Insecticide *Bacillus thuringiensis* var. *kurstaki* (*Btk*) on a Stream Benthic Community

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Richardson, J.S., and C.J. Perrin. 1994. Effects of the bacterial insecticide *Bacillus thuringiensis* var. *kurstaki* (*Btk*) on a stream benthic community. Can. J. Fish. Aquat. Sci. 51: 1037–1045.

Commercial formulations of the insecticidal bacterium *Bacillus thuringiensis* var. *kurstaki* (*Btk*) are frequently sprayed over bodies of water. The hypothesis that *Btk* poses a threat to stream communities was tested using streamside, flow-through mesocosms which received water and invertebrate colonists from a second-order stream in southwestern British Columbia; low (50 BIU/ha) and high (≥5000 BIU/ha) treatment levels were contrasted with controls. There were no significant differences in the density or composition of benthos sampled 7 d after *Btk* application. The densities were highest in the high-dose mesocosms. There were no significant differences in emergence rate of adults due to treatment. During the 2.5-h treatment, there were marginally elevated drift rates of the mayfly *Baetis* when exposed to the solution, but these differences were negated during the remainder of the 24-h period. Leaf packs lost significantly more mass in controls than in high-dose mesocosms, but there were no significant differences in the numbers of macroinvertebrates on those leaf packs. There was no evidence that addition of *Btk* to stream mesocosms created adverse effects for this benthic community, even at >100 times expected exposure rates.

Il arrive souvent que les formulations commerciales de la bactérie insecticide *Bacillus thuringiensis* var. *kurstaki* (*Btk*) sont appliquées sur des plans d'eau. Nous avons testé l'hypothèse que le *Btk* constituait une menace pour les communautés lotiques en l'essayant sur des mésocosmes installés au bord de l'eau et alimentés en continu avec de l'eau et des organismes colonisateurs invertébrés qui provenaient d'un cours d'eau de second ordre du sud-ouest de la Colombie-Britannique; on a comparé des cas témoins à des cas à faible dose de traitement (50 BUI/ha) et à forte dose de traitement (≥5 000 BUI/ha). Il n'y a pas eu de différence significative de densité ou de composition du benthos échantillonné sept jours après l'application du *Btk*. Les densités les plus élevées ont été observées dans les mésocosmes soumis à un traitement à forte dose. Quant à l'émergence des adultes, il n'y a pas eu de différence significative attribuable au traitement. Durant les 2,5 h de traitement, il y a eu un taux légèrement supérieur de dérive des éphémères *Baetis* exposées à la solution, mais ces différences n'ont pas été observées durant la suite des 24 h. Les lots de feuilles prélevés dans les stations-témoins ont perdu beaucoup plus de biomasse que ceux des mésocosmes exposés à de fortes doses de *Btk*; cependant, il n'y a pas eu de différence significative dans le nombre de macro-invertébrés observés sur ces lots. Rien n'indique que l'application de *Btk* à des mésocosmes lotiques a eu des effets nuisibles sur cette communauté benthique, même à des concentrations > 100 fois le taux d'exposition attendu.

Received July 2, 1993
Accepted November 26, 1993
(JB992)

Reçu le 2 juillet 1993
Accepté le 26 novembre 1993

Formulations of the insecticidal bacterium *Bacillus thuringiensis* (commonly abbreviated *Bt*) are increasingly being used as highly selective pesticides against a variety of pest organisms. There are several serovars or varieties of this bacterium, each of which has differing toxicity to particular groups of insects. *Bacillus thuringiensis* is a naturally occurring bacterium in the environment and is ubiquitous in soils around the world (Lambert and Peferoen 1992). The insecticidal properties of this bacterium come from the production of a parasporal protein body, also known as crystals, when the organism enters its spore stage (van Frankenhuyzen 1990; Lambert and Peferoen 1992). If a lethal dose of *Bt* spores with crystals is ingested by an insect, and if that insect has the appropriate gut biochemistry for digestion of the particular protein, and if the particular gut epithelial receptors are present, then the insect generally will die within 1–4 d (Lacey and Mulla 1990; van Frankenhuyzen 1990; Lambert and Peferoen 1992). The specificity of the toxin for particular groups of insects means that there are few of the environmental effects often seen with broad-spectrum chemical insecticides, such as nontarget species mortality and residual toxicity. Operational application of the insecticidal *Bt* has been widespread over the past decade in the treatment of forest pests (van Frankenhuyzen 1990) or insect vectors of human disease (Dejoux and Elouard 1990). Several varieties or serovars of *Bt* have been developed for their activity against particular insect pests, such as *B. thuringiensis* var. *kurstaki* (hereafter *Btk*) which is toxic to a variety of forest pest Lepidoptera including spruce budworm (*Choristoneura fumiferana*), jack pine budworm (*C. pinus*), gypsy moth (*Lymantria dispar*), and hemlock looper (*Lambdina fiscellaria*) (van Frankenhuyzen 1990). More than 3.2 million ha of forests in Canada were sprayed with *Btk* for control of pest Lepidoptera between 1985 and 1989, and use of *Btk* continues to increase (van Frankenhuyzen 1990).

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As the operational use of commercial formulations of *Btk* continues to increase, concerns about potential effects on nontarget organisms, including those in aquatic habitats, have increased. As part of routine *Btk* spraying, stream channels receive direct overspray plus that insecticide which may be lost from the riparian zone. Potential effects on nontarget organisms in streams are considered to be minor because of the specificity of the method of action of *Bt*. Nevertheless, since insects tend to dominate stream communities in terms of biomass, numbers, and species richness, any effect on these nontarget organisms could have implications for other values such as fish habitat capacity. There is evidence that *Btk* may have negative effects on some aquatic insects (Eidt 1985; Kreutzweiser et al. 1992), and thus there is concern for stream food webs, fish productivity, and ecosystem health.

Another variety of *Bt*, *B. thuringiensis* var. *israelensis* (*Bti*), is extensively used in streams to control black flies, and mosquitoes, e.g., as part of the World Health Organization's attempts to reduce densities of vectors of human disease. While *Bti* is fairly specific to black flies and mosquitoes, studies have shown negative effects on nontarget species (Merritt et al. 1989; Dejoux and Elouard 1990; Lacey and Mulla 1990), but these may have been due to trophic responses and food-web effects of black fly mortality (Wipfli 1992).

Much of the knowledge about the nontarget effects of *Btk* is based on acute toxicity laboratory tests. Widespread use of *Btk* in the field has allowed researchers to observe nontarget effects in terrestrial systems, but little is known of effects on aquatic organisms. A few studies have considered the effects of *Btk* on stream organisms, and these have been acute laboratory toxicity tests (Eidt 1985; Kreutzweiser et al. 1992). Eidt (1985) used a logarithmic dose intensity treatment in static toxicity tests with 2 times, 20 times, and 200 times normal spray concentrations and a control. Of the aquatic insects he tested, only larval *Simulium vittatum* showed significantly elevated rates of mortality over the 15-d experiment, and this was only at the highest dose rate. Black flies are often controlled using *Bti*, so perhaps there is some relation here. Larvae of one species of taeniopterygid stonefly had significantly elevated mortality due to *Btk* additions in laboratory toxicity tests at 100 times the expected field concentration (Kreutzweiser et al. 1992). Tests in ponds have shown no significant effect of *Btk* on pond invertebrates (Melin and Cozzi 1990).

Btk spores may persist in freshwater for several weeks. One estimate suggested a half-life for spore viability in a stream at 50 d (Melin and Cozzi 1990), and another study found viable *Btk* spores more than 70 d after addition to lake water (Menon and de Mestral 1985). One observation with *Bti* application in streams and laboratory microcosms is that the spores apparently chelate or adsorb to organic particles (Ohana et al. 1987; Dejoux and Elouard 1990). Given that detrital pathways are critical flows of energy in streams (Cummins et al. 1983), the concentration of spores adherent to organic particles may be cause for concern, especially in light of Kreutzweiser et al.'s (1992) observation of a significant increase in larval mortality of the detritivorous stonefly *Taeniopteryx* at exposure to extreme concentrations of *Btk*.

In this study, we used a replicated field experiment to test effects of additions of a commercial *Btk* formulation on a stream benthic community in flow-through mesocosms. We measured benthic densities, adult emergence, drift rates, and leaf pack decomposition in response to experimental application of the *Btk* suspension. In a trough mesocosm, biological processes are integrated, providing invertebrates with natural food levels and environmental conditions as they are in the natural stream, and this allows for replication and high levels of statistical power which enables considerable extrapolation of findings to larger stream reaches (Perrin et al. 1992). Our specific objectives were to test for any detrimental effect of additions of a formulation of *Btk* on survival, and behavioural responses of stream invertebrates, contrasted with control troughs. Another specific hypothesis was that given the adsorption of *Bt* spores and their toxin to organic particles, leaf packs of deciduous leaves would decompose slower when *Btk* was added if detritivores were able to detect and avoid high spore concentrations or if their feeding activities were otherwise deterred.

Methods and Materials

Study Site and Mesocosm Assembly

Stream mesocosms were established on the bank of Muir Creek, a second-order stream which drains westward from second-growth forest stands north of Sooke, on the southwest coast of Vancouver Island, British Columbia, Canada. Water temperatures were monitored daily on a maximum–minimum thermometer and were between 14 and 22.5°C, with temperatures decreasing slightly over the course of the experiment.

Each of the 15 mesocosm troughs (1.52 m long × 0.2 m high × 0.2 m wide) contained a gravel substratum that supported a representative stream benthic community. Water was supplied via a 15.24-cm-diameter pipeline that was laid upstream for a distance of about 200 m. The mesocosm design was similar to that originally described in Mundie et al. (1991, see their fig. 1) and Perrin et al. (1992). The water was delivered to each trough through a standpipe assembly that was adjusted to maintain water flow of approximately 500 mL/s in each trough and a surface current velocity of about 5 cm/s. The upstream end of each trough consisted of a mixing chamber having an angled baffle that created turbulence. Downstream of the mixing chamber was a 1.2-m section within which 2-cm-diameter drain rock was placed to a depth of 5 cm. This section supported the benthic community. A baffle placed at the downstream end of the gravel section controlled the water level and was set at 5 cm over the gravel surface.

Experimental Design

The experiment involved two treatments contrasted with a control with no addition of *Btk*: one treatment was a *Btk* addition at the high end of the range that might be expected in a small, shallow stream after routine spraying (i.e., 50 BIU/ha) and the other treatment was a high-level dose

TABLE 1. Arithmetic mean concentrations of *Bt* (±1 SE) in water samples collected from channel outflows during treatment and 4 d following treatment expressed as colony-forming units (CFU)/mL.

Date	Control	Low dose	High dose
27 August (during treatment)	27.4 (5.04)	2.1×10^4 (5.3×10^3)	1.8×10^8 (9.67×10^7)
31 August	4 (2.26)	8.17×10^3 (7.96×10^3)	332 (102.84)

≥100 times the previous rate. Each treatment was replicated five times resulting in a total of 15 experimental units (flow-through troughs). *Btk* was added as Foray 48B®, a commercially available aqueous concentrate that has a potency of 12.7 BIU/L. The low-dose rate of Foray® addition was calculated based on an aerial application rate of 50 BIU/ha to the area of a trough (0.3 m^2) with current velocity of 5 cm/s and water depth of 5 cm.

In most field applications, there is a limited window of direct application and transport in a stream. An application duration of 2.5 h fits this time course, mimics a worst-case scenario, and is close to that tested in other related studies (Eidt 1985; Kreutzweiser et al. 1992), thus allowing comparability between studies. Hence, transport in the water is likely to be transient, with elevated concentrations persistent on the order of 1 or 2 h. While the concentration of the related bacterium *Bti* has been shown to decline exponentially as the water moves downstream due to settling, filtration by invertebrates, and adsorption (Merritt et al. 1989; Chalifour et al. 1990), we chose a constant dose as an extreme case and because dose responses would be easier to interpret.

Colonization of the troughs by aquatic invertebrates began with the commencement of water flows on 16 July 1992. Invertebrates entered the system through the water supply and benthic communities developed in each trough by colonization of the substrata gravels. The discharge water during application was collected in a basin and pumped upslope to the forest floor. A single discharge line was branched to five separate lines to avoid channelization and pooling in depressions of the forest floor.

The Foray® treatments occurred on 27 August 1992. Stream water was used to dilute the *Btk* solution and stock solutions were kept in ten 3-L glass carboys, one for each trough receiving treatment. The three treatments were randomly assigned to the 15 troughs. The *Btk* solution was delivered to the low-level treatment troughs through a Technicon precision metering pump, and the high-dose troughs received the Foray® via Mariott tubes inserted into the appropriate glass carboy. The pump maintained a constant delivery rate of solution to the low-dose troughs; however, the Mariott bottles and tubes had to be recalibrated during the course of the application due to the high viscosity but were close to target levels throughout the 2.5-h treatment period.

Concentrations of viable *Btk* spores in the outflow of each trough were measured in water samples collected during treatment. A second set of water samples was collected 4 d later for a second count of *Bt* that may have been retained, perhaps in association with organic particles. The water samples were analyzed using the membrane filtration technique with plating on *Bacillus cereus* selective agar (EVS Consultants, North Vancouver, B.C.). Representative colonies were confirmed as *Bt* and counted using phase contrast microscopy. This method does not distinguish between varieties of *Bt*, but given the high rates of application in our experiment, most colonies can be attributed to *Btk*.

Drift has been used as a measure of behavioural and mortality responses to a manipulation in many studies, ecotoxicological and otherwise. Drift rates of stream insects from the troughs were determined during four 24-h periods, with starting dates of 21, 27, and 31 August and 2 September. On the first two dates (21 and 27 August), before and on the day of treatment, the drift periods were separated into 3 and 21 h to isolate immediate effects during the 2.5-h period of addition from nonimmediate effects, e.g., the night following additions. Most large invertebrates drift primarily at night and a severe exposure may be needed to overwhelm this behavioural predisposition. Drift was sampled with nets made of 250-μm-mesh Nitex® attached to the outflow of each trough. Using the replicated design, we contrasted the net differences in drift rate from each trough from before *Btk* addition to after addition (i.e., drift after minus drift before) and analyzed the data by treatment in a one-way ANOVA. Using the net difference assures the maintenance of the appropriate degrees of freedom, accounts for day to day differences across the experiment, and tests whether drift numbers changed more due to treatment than other sources of variation.

Emergence of adult insects was used as a measure of the ability of individuals to complete development and metamorphosis under experimental conditions. Emergent adult aquatic insects from the troughs were caught and preserved in Plexiglas® traps which covered the entire surface of the troughs. Adults were collected for a 1-wk period before treatment (12–19 August) and 1 wk following treatment (27 August to 3 September). Adults were identified to the family level and the differences (number after − number before) in emergence rate between dates was analyzed by treatment in a one-way ANOVA.

One week after *Btk* treatment, all benthic organisms were harvested from each trough by agitating the gravel in each trough for a standard period of 7 min and collecting the animals in 250-μm nets at the outflow. Samples were immediately preserved with 10% Formalin. In the laboratory the samples were sieved, and all organisms retained on 250- and 500-μm sieves were sorted from debris, identified to the lowest reliable taxonomic level, and counted. The data were tested for treatment effects using a one-way ANOVA for those taxonomic groupings where there were high enough densities to meet statistical assumptions (generally >30 animals per sample), and also for the numbers of taxonomic units (taxonomic richness).

Since *Btk* spores were expected to adhere to the surfaces of organic particles (Menon and de Mestral 1985), there was a danger that detritivores might ingest a concentration of the microbe that is higher than that in the water column, or *Btk* may affect other processes of leaf decomposition by

TABLE 2. Summary of taxa identified from experimental troughs on Muir Creek, British Columbia. Means (±1 SE for those taxa where numbers were high enough and with enough nonzero values to have meaningful parametric error terms) are shown for each taxon by treatment. Differences tested by one-way ANOVA. Benthos samples were sorted down to 250 μm. Some taxa were represented by only 1–10 specimens across the entire 15 troughs. These include *Malenka* (Plecoptera: Nemouridae), *Calineuria* (Plecoptera: Perlidae), *Hydropsyche* (Trichoptera: Hydropsychidae), *Dicosmoecus* and *Ecclisomyia* (Trichoptera: Limnephilidae), *Rhyacophila* (Trichoptera: Rhyacophilidae), *Hydrochus* (Coleoptera: Hydrophilidae), *Hexatoma* (Diptera: Tipulidae), and Tubificidae (Oligochaeta).

Order or class	Family	Genus, subfamily, or tribe	Controls	Low *Btk* dose	High *Btk* dose	Probability of no difference
Ephemeroptera	Baetidae	*Baetis*	584.6 (122.30)	562.4 (139.60)	729.6 (87.60)	0.57
		Centroptilum	10.4	3.4	6.4	
	Ephemerellidae		33.8 (3.11)	40.0 (9.79)	53.0 (5.63)	0.17
	Heptageniidae	*Rhithrogena*	5.2	20.0	5.0	
		Heptagenia				
	Siphlonuridae	*Ameletus*	11.2 (5.68)	10.8 (3.31)	7.8 (1.85)	0.80
	Leptophlebiidae	*Paraleptophlebia*	65.8 (10.37)	83.0 (8.86)	94.0 (10.50)	0.17
Plecoptera	Chloroperlidae	*Suwallia*	39.6 (10.02)	43.8 (8.83)	42.6 (13.97)	0.96
	Nemouridae	*Zapada*	4.2	6.2	6.4	
	Perlodidae	*Isoperla*	6.4	4.4	4.2	
Coleoptera	Elmidae	*Zaitzevia*	64.2 (14.95)	60.6 (9.06)	55.0 (4.34)	
Trichoptera	Hydroptilidae	*Agraylea*	21.2	24.2	42.0	
		Oxyethira				
	Lepidostomatidae	*Lepidostoma*	5.0	7.6	5.0	
	Polycentropodidae	*Polycentropus*	81.4 (12.81)	68.6 (16.47)	92.6 (20.77)	0.62
Diptera	Chironomidae	*Tanytarsini*	155.0 (42.21)	124.2 (50.69)	181.4 (16.59)	0.87
		Chironomini	410.2 (46.24)	442.0 (63.1)	637.4 (41.90)	0.02
		Diamesinae	0.2	4.2	0	
		Corynoneura	98.0 (12.50)	104.6 (31.57)	157.6 (15.3)	0.14
		Orthocladiinae (excluding *Corynoneura*)	236.8 (34.58)	202.4 (36.7)	326.0 (26.98)	0.05
		Tanypodinae	300.4 (45.01)	229.0 (34.95)	329.8 (44.27)	0.25
		Pupae	86.6 (7.62)	75.8 (13.39)	115.6 (8.96)	0.05
	Simuliidae		9.4 (2.46)	7.0 (2.17)	11.8 (4.83)	0.60
	Tipulidae	*Dicranota*	0.4	1.2	0.6	
	Ceratopogonidae		21.4 (8.73)	12.0 (4.00)	17.6 (4.83)	0.57
	Athericidae	*Atherix*	0.8	1.6	0	
	Dixidae		4.8	8.6	7.0	
Oligochaeta	Naididae		590.6 (41.47)	537.4 (71.76)	732.6 (75.92)	0.13
Totals			3054 (226.3)	2886 (266.7)	3668 (189.0)	0.08
Richness			17 (0.95)	18.6 (0.60)	17.6 (0.51)	0.31

fungi and bacteria. To test these possibilities, we used two leaf packs per trough composed of 5.0 g (±1%) of dried alder leaves as an assay for any detrimental effect particularly associated with detrital processing and detritivores. The leaf packs were added to the troughs on 6 August to allow 3 wk of incubation before treatment. At the end of the experiment the leaf packs were removed, invertebrates were washed from the leaves, and the invertebrates from one leaf pack of each trough were identified and counted in the laboratory. Each of the two leaf packs per trough, including any smaller particles in the leaf pack, were dried, weighed, ashed, and reweighed to determine ash-free dry mass (AFDM). The mean value of the two leaf packs per trough was used as the variable and tested for treatment effects with a one-way ANOVA. Likewise the data for invertebrates were analyzed by ANOVA for those groups where densities were sufficient for meaningful tests.

Results

Bacterial Counts

Counts of cultured colonies of *Bt* cells collected from each trough during the addition of the *Btk* formulation, and 4 d later, were analyzed by ANOVA of $\log_{10}(x + 1)$ transformed data. During application of *Btk*, counts from the high-*Btk*-dose troughs were >6 orders of magnitude above those of the controls and >3 orders of magnitude greater than in the low-dose troughs (Table 1). All three treatments were significantly different from each other (ANOVA, $p < 0.0001$, Scheffé's test). Bacterial counts remained elevated 4 d later in troughs that received *Btk* treatments (ANOVA, $p < 0.006$), and water from the high-dose treatment had concentrations statistically indistinguishable (Scheffé's test) from those in the low-dose troughs.

TABLE 3. Mean numbers (±1 SE) of animals within taxonomic and functional groups, total numbers, and number of taxa found per leaf pack in each treatment. Samples sorted to 250 µm. Differences between treatments tested by one-way ANOVA.

Grouping	Control	Low dose	High dose	Probability of no effect
Total numbers	157.6 (16.6)	169.8 (6.2)	157.6 (11.2)	0.71
Richness	17.2 (1.2)	19.0 (0.8)	16.6 (1.0)	0.28
Chironomini	41.6 (4.2)	45.4 (5.3)	39.4 (4.8)	0.67
Tanypodinae	13.6 (0.48)	12.4 (1.5)	11.8 (1.5)	0.62
Corynoneura sp.	15.2 (4.4)	21.8 (4.1)	11.0 (2.2)	0.15
Orthocladiinae (excluding *Corynoneura*)	15.8 (3.4)	9.4 (2.7)	16.8 (3.3)	0.23
Shredders	15.2 (4.7)	19.8 (5.4)	9.0 (1.4)	0.23

Benthos

The mesocosm supported a diverse and abundant benthic community. More than 40 taxa were found representing mayflies, stoneflies, beetles, caddisflies, chironomids, other true flies, worms, snails, nematodes, mites, ostracods, and even Cladocera (Table 2). Occasionally, terrestrial taxa were found in low numbers but they were not included. Midge larvae (Chironomidae) were the most abundant taxonomic grouping accounting for 39% of all invertebrates in the control troughs (Table 2). Larvae of the mayfly genus *Baetis* were the second most abundant taxon in the troughs accounting for 20% of all invertebrates. Although naidid worms (all between 250 and 500 µm) are often overlooked in stream studies, they represented about the same density as the baetid mayflies in Muir Creek. An average of 3200 animals were found in each trough, or about 10 500 animals/m^2 in the size fraction >250 µm. About a third of these animals were in the size fraction >500 µm. This density is typical of that found in natural streams.

No significant treatment effect was found for total benthic densities and number of taxa (ANOVA, $p > 0.05$; Table 2). Total densities were 20% higher in the high-*Btk*-dose troughs than in the control troughs, and about 75% of this difference was due to increased chironomid numbers. Fifteen taxonomic groups occurred in sufficient numbers for statistical analysis as listed in Table 2. The Chironomini, Orthocladiinae (excluding *Corynoneura*), and chironomid pupae appeared to increase significantly at the high dose of *Btk* (individual ANOVA's, $p \leq 0.05$; Table 2), but with application of the Bonferroni correction to avoid random effects in multiple comparisons (Rice 1988), the critical probability level was reduced to 0.003 (0.05 divided by 15 taxonomic groups), resulting in no statistically significant treatment effect. For all chironomid taxa, naidid worms, all mayflies except *Ameletus* sp., and the caddisflies, greatest mean abundance occurred with the highest dose of *Btk*, but there was no consistent ranking between the control and low dose. There was also no consistent ranking among the other taxa analyzed.

Since black fly larvae, and filter feeders in general, may ingest high numbers of spores during their feeding activities, and since black flies are susceptible to *Bti*, we analyzed numbers of simuliids and total filter feeders (including Simuliidae, *Hydropsyche*, and *Polycentropus*) separately. There was no significant effect of the *Btk* treatment (nontransformed or $\log_{10}$ transformed data) on either simuliids (ANOVA, $p > 0.6$) or all filter feeders ($p > 0.5$). Densities of black fly larvae and combined densities of filter feeders were highest in the high-*Btk*-dose troughs, followed by the controls and the lowest densities in the low dose (Table 2).

Leaf Packs

AFDM's of the alder leaf packs were determined for the two leaf packs per trough and the mean value per trough analyzed, except for one trough (a low-dose trough) for which only one complete leaf pack was available. Leaf packs were incubated for 3 wk prior to treatment and then for a further week posttreatment. There were significant differences in the leaf pack mass due to treatment (ANOVA, $p < 0.02$), with the high dose (2.68 g AFDM ± 0.031, mean and 1 SE) greater than the low dose (2.60 ± 0.065) and both greater than the controls (2.41 ± 0.056). Approximately half the starting leaf mass of 5 g was lost over the 4-wk incubation period in all troughs. An a posteriori comparison of means showed that the significant difference was between the leaf packs from the high-*Btk* treatment and the controls (Scheffé's test, $p < 0.05$).

Invertebrates on leaf packs were counted from one randomly selected leaf pack from each trough. Total numbers and the abundance of four taxonomic groups (Chironomini, Tanypodinae, *Corynoneura* sp., and Orthocladiinae (without *Corynoneura* included)) occurred in sufficient numbers for analysis. All other taxa occurred incidentally (i.e., <5 animals per sample) and were not separately analyzed. The numbers of taxa were also analyzed. Since leaf packs are the food source for "shredding" invertebrates (detritivores feeding on coarse particles), the total numbers of shredders per leaf pack were also tested for treatment effects. This functional group was selected based on the potential for exposure to adsorbed *Btk* spores and toxin on detrital particles. None of the taxonomic or functional groupings showed significant differences between treatments (ANOVA, all with $p > 0.15$; Table 3). The total numbers of invertebrates per leaf pack were highest from the low-*Btk*-dose troughs, and the other two treatments had identical mean numbers per leaf pack (Table 3). Numbers of the midge tribe Chironomini and the midge genus *Corynoneura* sp. (subfamily Orthocladiinae) were highest in the low-dose troughs, while the remaining orthoclads were lowest in the low-dose treatment (Table 3). The number of shredders showed no significant differences ($p = 0.23$), and the numbers were highest in low-*Btk* troughs, followed by controls, but numbers in the leaf packs in the high-dose troughs were less than half those of the low dose. There was no significant difference in the numbers of taxa per leaf pack ($p = 0.28$).

TABLE 4. Numbers of adults emerging per trough during the 1-wk period after treatment and the net difference between numbers for 1-wk periods before and after treatment. Probability of no treatment effect on the net difference based on ANOVA.

	Control		Low dose		High dose		
Grouping	After treatment	Net difference	After treatment	Net difference	After treatment	Net difference	Probability of no effect
Baetidae	51.2	42	67.8	39	43.2	48.6	0.84
Chironomidae	24	−11.4	28.6	−15.4	27.6	−12.8	0.9
Hydroptilidae	6	−4.6	12.4	−5.4	17.4	−15.8	0.4
Simuliidae	7.6	−8.4	10.8	−7	8.2	−2.8	0.2
Nemouridae	5	0.4	2.8	0.4	3.0	0.4	1.0
Total	97.6	18.8	128	21.4	103.4	21.4	0.92

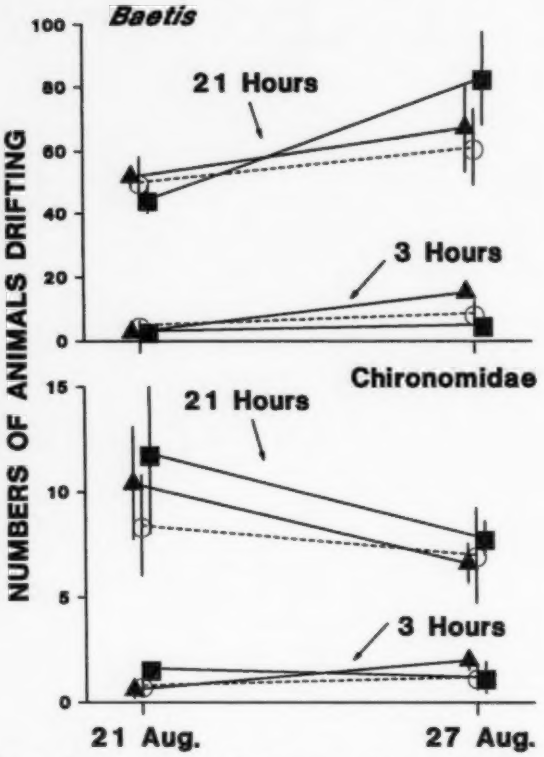

FIG. 1. Numbers of the mayfly *Baetis* sp. and larval Chironomidae collected in drift samples from the experimental troughs before (21 August) and during/after treatment of the appropriate troughs with *Btk* (27 August). Points represent means of the five troughs and have been slightly offset to separate the error bars (±1 SE). ■, controls; ○, low *Btk* dose; ▲, high *Btk* dose. The slopes of the lines remain appropriate for assessing differences before and after *Btk* additions. The lines are not meant to indicate a continuum of measures between the two points. Note the difference in scales on the *y*-axes.

Adult Emergence

Adults of the insect families Baetidae, Nemouridae, Chironomidae, Simuliidae, and Hydroptilidae emerged in sufficient numbers to allow statistical analysis. The difference in numbers emerged per trough from before treatment and after treatment was used to account for any systematic differences in troughs and maintain the appropriate degrees of freedom. There were no significant treatment effects for any of these taxa or for the total numbers of adults collected (ANOVA, all with $p > 0.2$; Table 4). There was also no consistent rank order of the numbers emerging by treatment.

Drift

Drift rate is defined as the number of animals leaving the troughs per unit time and can be regarded in this experiment as a measure of the behavioural response of stream animals to perturbation of their environment. The drift collections were made for a 3- and a 21-h period both before application of *Btk* and on the day of treatment. The 3-h sampling was organized to occur at the time of treatment. Only four groupings of data had sufficient numbers for analysis, and these were *Baetis*, larval Chironomidae, total number of drifting invertebrates, and the number of taxa represented. *Baetis* was the most abundant taxon in the drift samples followed by chironomid larvae, so most of the patterns detectable in total numbers drifting are largely based on responses by these two taxa.

There were no significant differences between troughs (based on their preassigned treatments) before application of *Btk* for either the 3- or the 21-h periods (Fig. 1) for any of the groupings of data (ANOVA, all with $p > 0.14$), thus confirming no trough effect on drift rates. To ensure trough effects were avoided over the time interval between measurements before and after treatment, statistical analyses used differences in numbers drifting before and after treatment.

During treatment, there was a significant increase ($p < 0.04$; Fig. 1) in 3-h drift rates of all invertebrates (mostly *Baetis* larvae), but not in the subsequent 21-h period ($p = 0.53$). Numbers of species drifting also increased with treatment ($p < 0.02$) but the net differences were as little as one taxon. An a posteriori test (Scheffé's test) showed that the 3-h drift from the high-dose troughs was significantly higher than the controls ($p < 0.05$) for *Baetis*, total invertebrates, and numbers of taxa. Drift rates from the low-dose troughs were not significantly higher than those of the controls (Scheffé's test). There was no significant effect of treatment on the drift rates of Chironomidae drifting during the 3-h application period as shown by lack of treatment interactions (indicated by differences in slopes) between dates in Fig. 1. There were no significant differences in the drift rates of any of the four groupings in the 21 h after treatment (ANOVA, all with $p > 0.50$), and drift rates from control troughs were slightly higher than from the treated troughs (Fig. 1).

Mortality due to toxic effects of the *Btk* formulation would be expected to show up to 1–4 d after exposure of the invertebrates. Drift samples (24-h duration) from 1 and 3 September showed no significant differences in drift rates for any of *Baetis*, Chironomidae, total invertebrates, or taxonomic richness. There were no consistent patterns in the order of drift rates between treatments (Fig. 2). For example, on 1 September, total numbers drifting were highest from the controls, but on 3 September, total numbers from the controls were lowest of the three treatments.

Another approach to examine treatment effects on drift rates is to examine per capita drift rate, i.e., the ratio of numbers drifting per unit time to benthic abundance. It may also be considered a rough estimate of "turnover time". Since *Baetis* was the most common taxon in drift, we used it to examine the influence of *Btk* additions on per capita drift. During the 3-h drift sample during treatment, per capita drift rates of *Baetis* were 1.2% for the controls (based on densities from the end of the experiment), 3.7% in troughs receiving the high dose, and 2.3% for the low dose. In the subsequent 21 h the rates were highest in the controls at 19.0%, followed by the high-dose troughs with 16.1% and the low-dose at 15.7%. The combined 24-h per capita drift rate on the day and night of treatment was higher for the controls, followed by the high dose and the low-dose treatments. Since *Baetis* accounts for most of the drift, this comparison shows that there was no change in turnover time or net emigration associated with the *Btk* addition, at least for the 24-h period.

Discussion

Most of the measures from our experiment showed no significant effect of the application of *Btk* on a benthic stream community even at 100 times the highest operational dose rate. Indices of community structure and processes including benthos abundance, numbers of animals associated with leaf packs, adult emergence, and drift rates did not change significantly in response to the *Btk* treatments. In fact, final benthic densities for most taxa were highest in the high-*Btk*-dose troughs. The mesocosms provided conditions of food and abiotic environment suitable for aquatic invertebrates, and 7 d posttreatment should have been sufficient to see any losses to increased mortality, since *Btk* usually has its toxic effect within 3–4 d (van Frankenhuyzen 1990).

One observation indicated that catastrophic drift behaviour may be associated with the high-*Btk* dosing. There was an increase in short-term (3-h) drift of *Baetis* with the onset of treatment. Assuming the final benthic densities of this mayfly were similar to the density at the time of *Btk* additions (1 wk earlier), the 3-h per capita drift rates were 0.0119 in the controls and up to 0.037 in the high-dose treatment. While drift rates tripled in the high-dose relative to control troughs, the nighttime per capita drift rates measured in the following 21 h were 0.16 in the low- and high-dose treatments and 0.19 in the controls. Thus, there was no residual effect after the actual application and, in fact, drift rate for the 24-h period that included the 2.5 h of *Btk* additions was actually higher in the controls than in the treatment troughs. Since *Baetis* larvae made up the largest proportion of the drift, the effect noted in the total numbers is attributed mainly to this mayfly. Since there was no treatment effect on *Baetis* in benthos (Table 2), these per capita drift data suggest that the elevated drift rate was a short-term response, perhaps related to increased turbidity that occurred with the addition of the high dose of *Btk* or due to ingredients in the *Btk* formulation (see below). There was no increase in drift rates in the days following the treatment as might be expected if there was delayed mortality due to toxic effects of ingestion of the insecticide.

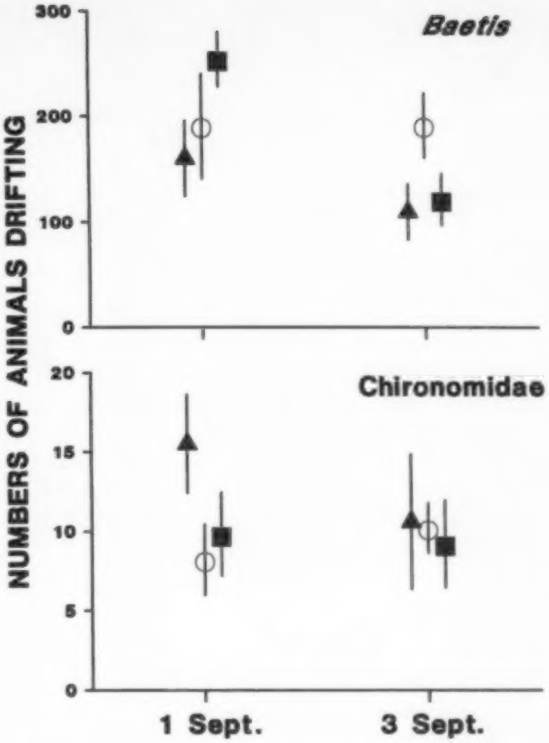

FIG. 2. Numbers of the mayfly *Baetis* sp. and larval Chironomidae collected in drift samples for 24-h periods 5 and 7 d after treatment of the appropriate troughs with *Btk*. Points represent the means of the five troughs per treatment and have been slightly offset to separate the error bars (±1 SE). ■, controls; ○, low *Btk* dose; ▲, high *Btk* dose.

One of our initial hypotheses was that leaf packs would decompose more slowly if *Btk* particles adsorbed onto the surface of the leaf tissue and this somehow deterred the feeding activity of shredders. Since bacterial counts were still higher in water from the treated troughs 4 d after treatment, it is clear that adsorption occurred and that Foray® was released to the water column from adsorption sites over time, either in association with sloughed particles or by desorption. While there was more leaf tissue remaining in the troughs receiving *Btk*, the data do not support our original hypothesis, since there was no significant treatment effect on the number of shredders on leaf packs. We cannot reject this hypothesis entirely, since shredder density on leaf packs was lower in high-dose troughs, but we suggest some further possibilities. First, there could have been some negative interaction between the bacterial insecticide or its carrier solution and the fungi and bacteria associated with the decaying leaf tissue. Since densities of "shredders" were an order of magnitude lower than in smaller coastal streams that have greater influence from detrital processes (Richardson 1992), most of the decomposition was likely due to microbes and these may have been adversely affected. A second possibility is that detritivorous invertebrates may have been feeding on the *Btk* particles or the starchy matrix adsorbed to the leaf surface and thereby ate less of the leaf tissue itself. Testing these hypotheses would require more detailed microbial experiments and feeding studies.

There have been other tests of the effects of *Btk* application on freshwater organisms. In an experiment in flow-through troughs, Kreutzweiser et al. (1992) found no significant effect of *Btk* application on drift or mortality rates of aquatic insects even at an application rate 100 times that expected under field conditions. However, in a laboratory toxicology experiment, there was a significant increase in the mortality rate of the detritivorous stonefly *Taeniopteryx nivalis* (Kreutzweiser et al. 1992), which is one of the reasons we considered effects of *Btk* application on shredders and leaf pack decomposition. In a field study, net-spinning hydropsychid (Trichoptera) larvae were collected with concentrated spores of *Btk* in their guts with no apparent toxic effects (Melin and Cozzi 1990). The only other study to have examined the effect of *Btk* on stream insects was a static toxicity bioassay in which black fly larvae, especially *S. vittatum*, showed a significant increase in mortality relative to controls at the highest dose of *Btk*, which was 200 times the expected environmental concentration (Eidt 1985). We found no negative effect of *Btk* application on black flies or filter feeders in terms of final densities and the numbers of emergent adult black flies.

Adverse effects of fish exposure to *Bti* or *Btk* have been shown to be due to formulation components rather than the bacterial toxin itself, since fish lack the gut biochemistry for any direct toxic effects. High concentrations of *Bt* formulations can cause gill clogging and suffocation (Snarski 1990; Wipfli 1992; R. Watts, Environment Canada, North Vancouver, B.C., personal communication). Preservatives in the formulation, such as xylene (Fortin et al. 1986), or high acidity (R. Watts, personal communication) is the likely culprit of toxicity towards fish at extremely high concentrations tested in laboratory assays. Nevertheless, commercial formulations of *Bti* had the lowest level of toxic effect of any of a series of pesticides tested on the mummichog (*Fundulus heteroclitus*) (Lee and Scott 1989).

One of the other ways that sublethal effects may propagate through ecosystems in through food-web effects. There were no obvious negative effects of *Btk* in our study, nor in that of Kreutzweiser et al. (1992) which would have suggested possible food-web effects. Studies of the black fly and mosquito larvicide *Bti* have shown potential for food-web effects. For instance, while Merritt et al. (1989) found no significant effects of *Bti* treatment on density or growth of most stream invertebrates (other than the target black flies), there was a significant increase in mortality of the tanytarsine midge *Rheotanytarsus*, another filter feeder, with a mortality rate of 27%. There were also food-web effects of *Bti* application on growth rates of some species of invertebrates in field mesocosms due to changes in abundance and ease of capture of moribund black fly larvae (Wipfli 1992). Such effects are unlikely to occur due to exposure to *Btk* based on the results of our experiment.

Our experiment found only minor evidence of any effects of experimental application of *Btk* to a benthic stream community, and those effects noted were not obviously detrimental. In fact, the final benthic densities, particularly of the chironomids, reached their highest levels in troughs having received a dose of the formulation more than 100-fold higher than could be expected from operational spraying over a small and shallow coastal stream. This study provides evidence that *Btk* is not harmful to benthic stream invertebrates under operational field application. The small, but statistically significant, reduction in decomposition of leaf packs demonstrates that there are ecosystem processes which are affected by *Btk*, but the relevance of these changes requires longer term and larger scale experiments.

Acknowledgements

Mr. John Henigman was instrumental in initiating this project and securing funding. John Henigman, Steve Samis, Mike Wan, Dan Cronin, and Sylvia von Schuckmann provided feedback on an early version of the report. We are grateful for the assistance of Mr. Ian Booth, who did much of the field work for this project, and Mr. Rick Irvine. Dr. Ron Griffiths sorted, identified, and counted the benthic and drift samples, and Mr. Jordan Rosenfeld identified and counted the emergent adult insects. Margot Daykin of EVS Consultants completed the *Btk* counts from the water samples with advice from Judy Smith of the Greater Vancouver Water District. This application of *Btk* was approved as per Water Management Approval No. 636 issued under section 7 (1) (a) of the Water Act of British Columbia. We appreciate comments on the manuscript by Dr. R.W. Merritt, Dr. J. Harold Mundie, Dr. Mark S. Wipfli, and an anonymous reviewer. Funding was provided by the British Columbia Ministry of Forests.

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Fish Distribution and Catchability: What Is the Appropriate Measure of Distribution?

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Swain, D.P., and A.F. Sinclair. 1994. Fish distribution and catchability: what is the appropriate measure of distribution? Can. J. Fish. Aquat. Sci. 51: 1046–1054.

Catchability to commercial fisheries has been predicted to be density dependent due to density-dependent variation in stock area. Previous studies have used indices of stock area based on thresholds of absolute density. These indices will increase with abundance even if density increases uniformly over all areas. We show that spatially uniform changes in abundance can affect catchability given certain models for the distribution of fishing effort, but that this effect is slight compared with the effect of changes in the spatial spread of fish distribution. We describe an index of distribution that depends only on spatial spread: the minimum area over which a specified percentage of the population is spread. We tested the density dependence of this index using data on Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Results depended on the percentage of the population for which the index was evaluated. The area containing most (90 or 95%) of the population was density dependent, expanding as population size increased. The area of highest cod concentration (i.e., the area containing 50% of the population) did not expand significantly as population size increased.

On a prédit que le potentiel de capture dans des pêches commerciales dépendait de la densité du fait qu'il y avait une variation elle-même dépendante de la densité de la superficie occupée par le stock. De précédentes études ont appliqué des indices de superficie occupée par les stocks qui étaient établis à partir de seuils de densité absolue. Ces indices progressent avec l'abondance même si la densité s'accroît uniformément dans tous les secteurs considérés. Nous prouvons que les changements d'abondance qui s'exercent uniformément dans l'espace peuvent agir sur le potentiel de capture si l'on prend certains modèles de répartition de l'effort de pêche, mais que cet effet est mince à comparer à l'effet des changements de l'étalement spatial de la distribution des poissons. Nous décrivons un indice de distribution qui dépend seulement de l'étalement spatial : la superficie minimale sur laquelle un pourcentage donné de la population est étalé. Nous avons testé la dépendance avec la densité de cet indice au moyen de données sur la morue franche (*Gadus morhua*) obtenues dans la partie sud du golfe Saint-Laurent. Les résultats dépendaient du pourcentage de la population en fonction duquel l'indice était évalué. La superficie occupée par la majeure partie de la population (90 ou 95 %) dépend de la densité et s'accroît à mesure que la population augmente. La superficie correspondant à la plus forte concentration de morue (c.-à.-d. la superficie qui est occupée par 50 % de la population) ne s'est pas accrue significativement à mesure que la population a augmenté.

Received July 28, 1993
Accepted December 10, 1993
(JC024)

Reçu le 28 juillet 1993
Accepté le 10 décembre 1993

Catch rates (catch-per-unit-effort) in commercial fisheries have often been used to provide information about changes in fish abundance. A critical assumption underlying this use of catch rates is that catchability, the proportion of a population captured by a unit of effort, is constant. Paloheimo and Dickie (1964) defined catchability (q) as

$$(1)\qquad q = ca/A$$

where a is the area swept by a unit of effort, c is the probability that a fish in the swept area will be caught by the fishing gear, and A is the area over which the total population is distributed. Thus, given this definition, q is inversely proportional to the area occupied by a stock. Paloheimo and Dickie (1964) concluded that catch rates cannot provide a measure of variation in abundance unless additional information on fish distribution is available.

Theoretical models of habitat selection predict the expansion of geographic range with increasing population abundance (reviewed by MacCall 1990). This range expansion is predicted when individuals begin to occupy "poorer" habitats as abundance and competition increase in "better" habitats. On the other hand, once all suitable habitats are occupied, some models predict that density will increase uniformly in all habitats as population abundance increases, so that the proportion of the population in each habitat will be independent of population size (e.g., "input matching", reviewed by Parker and Sutherland 1986). Empirical tests of the relationship between abundance and geographic range of fish stocks have been equivocal. Positive correlations between stock area and abundance have been reported for a number of stocks (e.g., Winters and Wheeler 1985; Crecco and Overholtz 1990; MacCall 1990; Rose and Leggett 1991; Swain and Wade 1993; Marshall and Frank 1994), although not for others (e.g., Murawski and Finn 1988; Marshall and Frank 1994). If abundance and geographic range are posi-

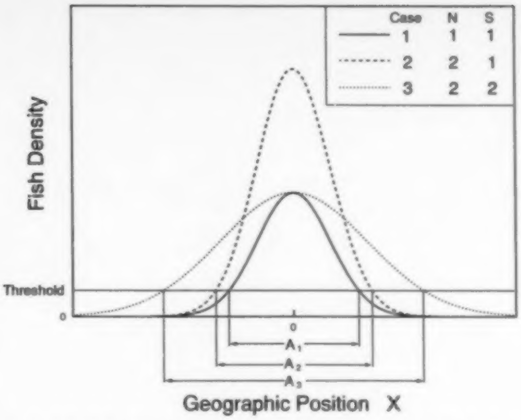

FIG. 1. Model of spatial variation in fish density. Fish density at geographic position x is given by equation 2 in the text. Three cases are shown, illustrating effects of changes in abundance N and spatial spread S on stock area A when stock area is defined as the area over which absolute density exceeds some constant threshold. Stock area increases from A_1 to A_2 when density increases uniformly over all areas (case 2 versus case 1: no change in S). A greater increase in stock area (A_1 to A_3) occurs when density increases nonuniformly in a manner consistent with density-dependent habitat selection (case 3).

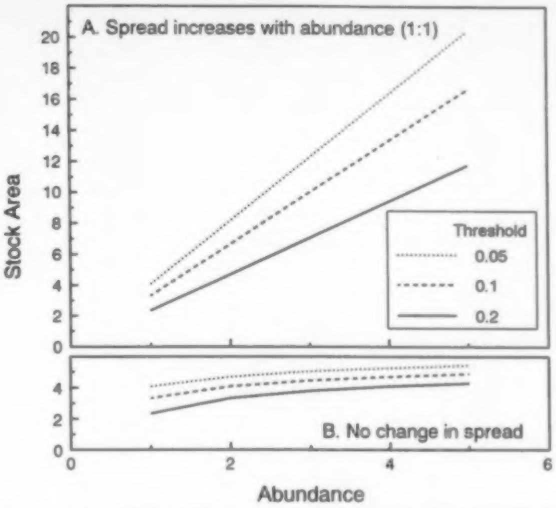

FIG. 2. Effects of spatially (A) uniform and (B) nonuniform changes in abundance on stock area, when stock area is defined as the area over which absolute density exceeds some constant threshold. Stock areas calculated using the model described in Fig. 1 and the text (equation 2). Maximum fish density is 0.4 when abundance is 1. In Fig. 2A, spatial spread S increases at the same rate as abundance N (e.g., cases 1 and 3 in Fig. 1). In Fig. 2B, spread is held constant ($S = 1$) as abundance increases (e.g., cases 1 and 2 in Fig. 1).

tively correlated, then equation 1 predicts that catchability should increase as population size decreases. This prediction has serious implications for stock assessment and fisheries management.

One assumption underlying equation 1 is that fish are uniformly distributed over the stock area A. In this case, changes in stock area involve changes in the "spread" of fish spatial pattern. Paloheimo and Dickie (1964) recognized that fish are not likely to be uniformly distributed over their range. The definition of stock area becomes problematic in this case of heterogeneous fish distributions. Previous studies have used indices of stock area based on thresholds of absolute density. Crecco and Overholtz (1990) and Swain and Wade (1993) used the geographic area over which estimated fish density exceeded the long-term (20 yr) 50th and 60th percentile (respectively) of the catch per tow in annual research surveys. Rose and Leggett (1991) used the percentage of hydroacoustic transects with estimated density greater than 10 cod/km. Others have used the average distance of all nonzero sets from the annual center of distribution or from a fixed reference point (Murawski and Finn 1988; Marshall and Frank 1994). When defined in terms of such thresholds of absolute density, stock area will be affected by spatially uniform changes in abundance as well as by changes in spatial spread if fish density varies over the range (Fig. 1). Changes in spread will have a much greater effect on stock area than will spatially uniform changes in abundance (Fig. 2). However, the effect of spatially uniform abundance changes will increase with the density used to define stock area and can be substantial when a high density threshold is used. For example, in the model in Fig. 1 and 2, a fivefold spatially uniform increase in abundance nearly doubles stock area when the threshold is 0.2, half the maximum density at the lowest level of abundance. Previous demonstrations of increases in groundfish stock area with abundance (Rose and Leggett 1991; Swain and Wade 1993) have involved increases in spatial spread rather than spatially uniform changes in abundance (see Discussion). However, spatially uniform changes in groundfish abundance have been demonstrated in other cases (Myers and Stokes 1989).

One purpose of this paper is to examine the relationship between stock area and catchability when fish are not uniformly distributed over their range. In this case, catchability will depend on the distribution of fishing effort relative to the distribution of fish. Using three simple models of the distribution of fishing effort in relation to the distribution of fish, we compare effects of changes in spatial spread versus spatially uniform changes in fish density. We show that spatially uniform changes in abundance can affect catchability given certain models for the distribution of fishing effort but that this effect is slight compared with the effect of changes in spread.

An index of stock area that depends only on the spread of fish spatial pattern is needed to test the predictions of theoretical models of habitat selection (e.g., MacCall 1990) and to test for effects of spatial spread on catchability (Paloheimo and Dickie 1964). One approach has been to select a very low absolute density as the threshold that delimits stock area (Murawski and Finn 1988; Marshall and Frank 1994). This approach reduces but does not in principle eliminate changes in stock area when changes in abundance are spatially uniform. A second purpose of this paper is to describe a new measure of stock area that depends only on the spatial spread of fish distributions. We examine the density dependence of this new statistic using data for Atlantic cod (*Gadus morhua*) in the southern Gulf of

St. Lawrence and compare our results with those obtained using stock areas based on thresholds of absolute density.

Methods

Effects on Catchability

We compared effects of spatially uniform and nonuniform changes in density on catchability. We refer to these as effects of "abundance" and "spread", respectively. We modelled spatial heterogeneity in fish distribution using the normal distribution. Mean geographic position was set at 0. Changes in spatial spread were modelled by changes in the standard deviation S of geographic distribution. Spatially uniform changes in abundance were modelled by multiplying the normal density by a scaling factor N. That is, we calculated fish density at geographic position x (d_x) as

$$(2) \qquad d_x = \frac{N}{S\sqrt{2\pi}} e^{-\frac{x^2}{2S^2}}$$

Examples with $N = 1$ or 2 and $S = 1$ or 2 are shown in Fig. 1. Catch rate at geographic position x (U_x) is given by

$$(3) \qquad U_x = cad_x$$

where c and a are defined as above. Catchability at position x (q_x) is given by

$$(4) \qquad q_x = \frac{U_x}{N}$$

where N is population size.

We examined three simple models for the distribution of fishing effort. In model I, fishing effort was distributed randomly over the area where fish density exceeded some constant threshold. In model II, fishing effort was distributed in proportion to fish density (i.e., an area with $X\%$ of the fish received $X\%$ of the fishing effort). In model III, all fishing effort occurred in the area with the highest fish density. These models were chosen to span the range of possible fishing behaviours and are not likely to apply to any real fishery. Model III is one extreme where fishermen have perfect knowledge of fish distribution and are unconstrained by factors such as competition and travel costs. Model I is the other extreme where fishing is conducted without regard to fish density as long as it exceeds some minimum level. Model II is intermediate and is the distribution predicted by some simple optimal foraging models (e.g., input matching, see Parker and Sutherland 1986).

Given model I, average catch rate is

$$(5) \qquad \overline{U} = \frac{caN \int_{-x_T}^{x_T} f(x)\,dx}{x_T - (-x_T)} = \frac{caN \int_{0}^{x_T} f(x)\,dx}{x_T}$$

and average catchability is

$$(6) \qquad \overline{q} = \frac{ca \int_{0}^{x_T} f(x)\,dx}{x_T}$$

where $f(x)$ is the normal density function and x_T corresponds to the fish density d_T above which fishing occurs (Fig. 3).

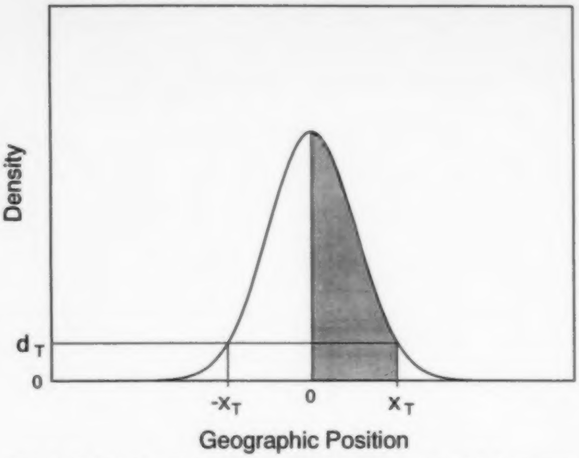

FIG. 3. Calculation of average catchability given model I fisherman behaviour. d_T is the density threshold above which fishing occurs. The area over which fishing occurs is $-X_T$ to X_T. Average catch rate is a constant times the shaded area divided by X_T (see equation 4 in the text).

Given model II, the proportion of fishing effort occurring at position x is $f(x)$. Thus, average catchability is given by

$$(7) \qquad \overline{q} = ca \int_{-\infty}^{\infty} f(x) \frac{Nf(x)}{N} dx = ca \int_{-\infty}^{\infty} (f(x))^2\,dx.$$

We integrated this equation numerically using Romberg's method (Press et al. 1989).

Given model III, all fishing occurs at $x = 0$. In this case, average catchability is given by

$$(8) \qquad \overline{q} = c\,a\,f(0) = \frac{ca}{S\sqrt{2\pi}}.$$

In order to examine effects of spatially uniform changes in abundance, we calculated q holding S constant ($S = 1$) and varying N between 1 and 10. In order to examine effects of changes in spatial spread, we calculated q holding N constant ($N = 1$) and varying S between 0.5 and 4. Calculations using model I were performed for each of three density thresholds ($d_T = 0.05$, 0.1, or 0.2). With $d_T = 0.2$, we report q for values of S up to only 1.5 because no fish densities reached 0.2 with $N = 1$ and $S = 2$ or more. With $d_T = 0.1$, the maximum S that we could use with model I and $N = 1$ was 3.5. For all cases, catchability is reported relative to the value for model II with $S = 1$ and $N = 1$.

Index of Distribution

Our objective was to develop an index of distribution that depends only on spatial spread and not on overall abundance. One such index is the area within which $x\%$ of the population occurs. We calculated this index for cod in the southern Gulf of St. Lawrence using data from bottom trawl surveys conducted in the southern Gulf each September. These surveys have been conducted since 1971 using a stratified random design. Survey procedures are described in Hurlbut and Clay (1990) and summarized in Swain and Wade (1993). For each year from 1971 to 1991 and each age from 3 to 8^+, we calculated cumulative frequencies of cod catch:

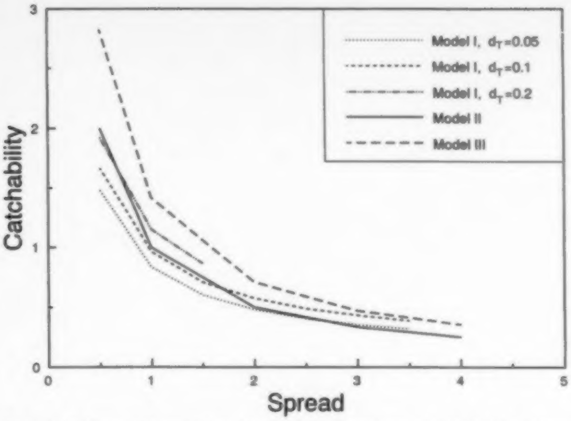

FIG. 4. Effects of variation in spatial spread on catchability when abundance is held constant.

$$(9)\qquad F(c)=100\frac{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}X_{hi}I}{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}X_{hi}}\qquad \text{where } I=\begin{cases}1 \text{ if } X_{hi}\le c\\ 0 \text{ otherwise}\end{cases}$$

where A_h is the area of stratum h, n_h is the number of trawl tows in stratum h, X_{hi} is the number of cod caught in tow i in stratum h (standardized to a tow length of 1.75 nautical miles), L is the number of strata, and c is a level of cod density (i.e., number per standard tow).We also calculated cumulative area in relation to cod catch:

$$(10)\qquad G(c)=\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}I\qquad \text{where } I=\begin{cases}1 \text{ if } X_{hi}\le c\\ 0 \text{ otherwise.}\end{cases}$$

We evaluated F at intervals of 0.1 and calculated the 5th, 10th, 25th, and 50th percentiles of cod catch (Sokal and Rohlf 1981, p. 46). We calculated the area associated with each of these levels of cod catch from G and an index of distribution D_x as

$$(11)\qquad D_x = A_T - G(c_{100-x})$$

where A_T is the total area surveyed and c_{100-x} is the 100 − xth percentile of cod catch. For example,

$$D_{95} = A_T - G(c_{05})$$

where c_{05} is the 5th percentile of cod catch and $G(c_{05})$ is the area over which cod density is at or below the 5th percentile level. D_{95} can be thought of as an estimate of the minimum area over which 95% of the population is distributed. A_T was 70 075 km^2, except in 1978 when only 63 608 km^2 were surveyed and in 1983 and 1988 when 68 945 km^2 were surveyed. For these three years when not all strata were sampled, the calculated values of D_x were standardized to a total area of 70 075 km^2. We calculated D_x for x equal to 95, 90, 75, and 50.

We tested the density dependence of D_x using midyear population sizes calculated from data given in the latest assessment of this stock (Chouinard et al. 1993). For each age group i, we compared D_x with (1) N_i, the abundance of age-i cod, (2) NA$_i$, the abundance of cod aged $i - 1$ to $i + 1$ (3–4 for $i = 3$, 7–8$^+$ for $i = 8^+$), and (3) NT, 3$^+$ abundance. We used Pearson product-moment correlations as a measure of the association between distribution and abundance. For each group of six tests (i.e., $i = 3$–8^+), we controlled the groupwide type-1 error rate using sequential Bonferroni comparisons (Rice 1989).

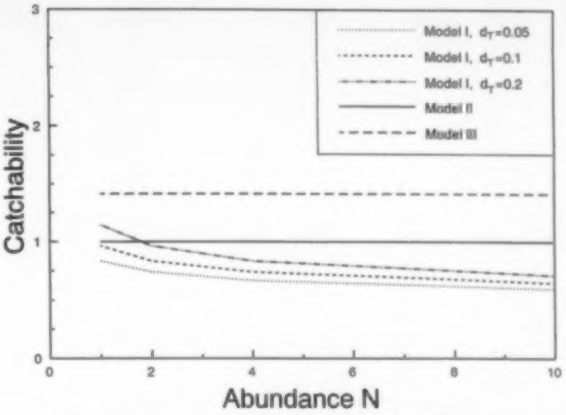

FIG. 5. Effects of variation in abundance on catchability when spatial spread is held constant.

Plots of D versus N suggested an asymptotic relationship for D_{95} but not for D_{50}, particularly for the older age groups (see Fig. 7 and 8). Thus, we also compared D_{95} and N using an asymptotic regression model:

$$(12)\qquad D = \beta_0 - \beta_1 (\exp(-\beta_2 N)).$$

This allowed comparisons with the results of Swain and Wade (1993), who used this model to test for an effect of population size on stock area (defined as the area over which estimated density exceeded a constant absolute threshold).

Results

Effects on Catchability

Average catchability declined sharply as the spatial spread of fish distribution increased for all three models of fishing effort distribution (Fig. 4). The decline in catchability was more pronounced for models II and III than for model I. This is because fishing effort is more concentrated in areas of high catch rate in models II and III than in model I.

Given the assumption of spatially uniform changes in abundance, average catchability was independent of abundance level for models II and III (Fig. 5), as can be seen in equations 7 and 8. In model I, average catchability declined as abundance increased (Fig. 5). This was because fishing under model I occurs further into the tails of the fish distribution as abundance increases. However, even under model I, declines in catchability with spatially uniform increases in abundance were slight compared with declines in catchability resulting from increasing spatial spread.

Index of Distribution

The areas occupied by 50–95% of cod in the southern Gulf varied considerably among years (Fig. 6). The area occupied by 90 or 95% of cod tended to vary more widely than the area occupied by 50% of cod. For younger cod (especially age 3), D_{90} and D_{95} tended to be low in the early to mid-1970's, high in the early to mid-1980's, and low in

TABLE 1. Correlation between the distribution index D_x and abundance of cod in the southern Gulf of St. Lawrence. D_{xi} is the estimated minimum area within which *x*% of age-*i* cod occur. N_i is the estimated abundance of age-*i* cod, NA_i is the abundance of cod of age $i - 1$ to age $i + 1$ (ages 3 and 4 for $i = 3$, 7 and 8^+ for $i = 8^+$), and NT is the abundance of cod aged 3 and older. Boldface indicates groupwide ($n = 6$) significance at the 0.05 level according to a sequential Bonferroni test.

		D_{95}			D_{90}			D_{75}			D_{50}		
Age		N_i	NA_i	NT	N_i	NA_i	NT	N_i	NA_i	NT	N_i	NA_i	NT
3	*R*	0.51	0.54	0.61	0.52	0.55	0.60	0.48	0.47	0.45	0.53	0.46	0.34
	P	**0.020**	**0.011**	**0.0035**	**0.016**	**0.010**	**0.0040**	0.027	0.030	0.038	0.014	0.035	0.13
4	*R*	0.64	0.66	0.74	0.64	0.66	0.71	0.53	0.55	0.58	0.34	0.36	0.30
	P	**0.0016**	**0.0010**	**0.0001**	**0.0017**	**0.0011**	**0.0003**	0.013	0.0098	**0.0054**	0.13	0.11	0.19
5	*R*	0.51	0.66	0.63	0.47	0.64	0.63	0.22	0.44	0.45	−0.10	0.08	0.12
	P	**0.017**	**0.0012**	**0.0023**	**0.033**	**0.0016**	**0.0022**	0.34	0.044	0.040	0.65	0.73	0.62
6	*R*	0.60	0.60	0.57	0.54	0.52	0.55	0.35	0.32	0.42	0.16	0.13	0.28
	P	**0.0038**	**0.0039**	**0.0075**	**0.012**	**0.015**	**0.0097**	0.12	0.15	0.059	0.49	0.56	0.21
7	*R*	0.55	0.65	0.60	0.50	0.57	0.55	0.36	0.38	0.41	0.13	0.14	0.31
	P	**0.010**	**0.0014**	**0.0042**	**0.022**	**0.0070**	**0.0095**	0.11	0.091	0.062	0.59	0.55	0.17
8^+	*R*	0.60	0.66	0.55	0.60	0.65	0.55	0.48	0.53	0.52	0.34	0.36	0.37
	P	**0.0040**	**0.0012**	**0.0093**	**0.0044**	**0.0013**	**0.0097**	0.026	0.013	0.015	0.14	0.11	0.096

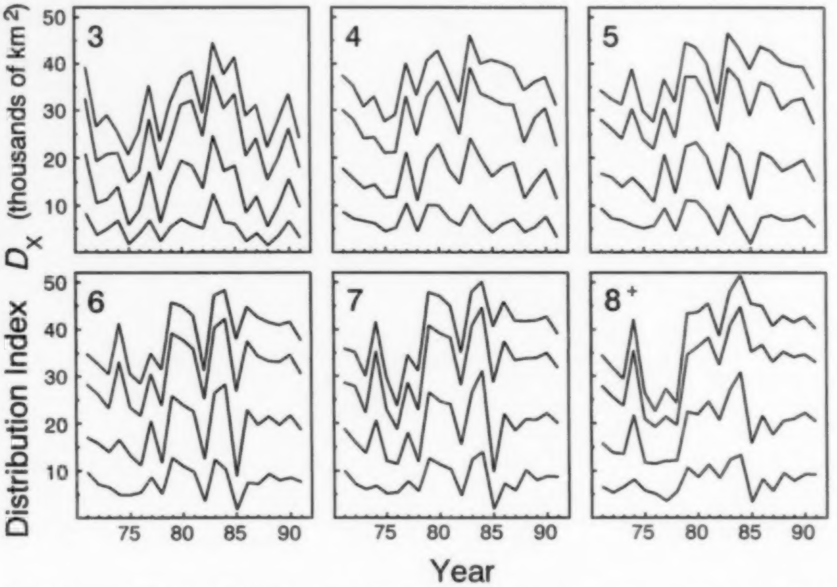

FIG. 6. Annual variation in distribution indices D_{50}, D_{75}, D_{90}, and D_{95} (bottom line to top line) for ages 3–8^+ of cod in the southern Gulf of St. Lawrence. D_X is the minimum area over which *X*% of the population is spread.

recent years. For older cod (especially ages 7 and 8^+), D_{90} and D_{95} tended to be low in the mid- to late 1970's and high in the 1980's.

The density dependence of cod distribution depended on age and the level for which *D* was evaluated (Table 1). D_{95} and D_{90} were strongly density dependent, increasing as abundance increased for all ages of cod (Fig. 7). Results were similar regardless of the measure of abundance used. Correlations with NA tended to be slightly stronger than those with *N*. Correlations with NT tended to be slightly stronger than those with *N* for younger cod but not for older cod. All correlations were significant according to both single-test probability levels and Bonferroni comparisons. These results indicate that the area containing 95 or 90% of cod tended to increase as abundance increased. That is, at these percentiles, cod distribution tended to spread out as abundance increased.

For older cod (ages 6–8^+), an asymptotic model fit the relationship between D_{95} and *N* better than a linear model (Table 2). Estimated asymptotes ranged from 35 102 km^2 for age-3 cod to 44 479 km^2 for age-8^+ cod. The increase in distributional area with increasing abundance was steepest for older cod. Variation in abundance explained 31–52% of the variation in distributional area (i.e., D_{95}) using an asymptotic model (Table 2).

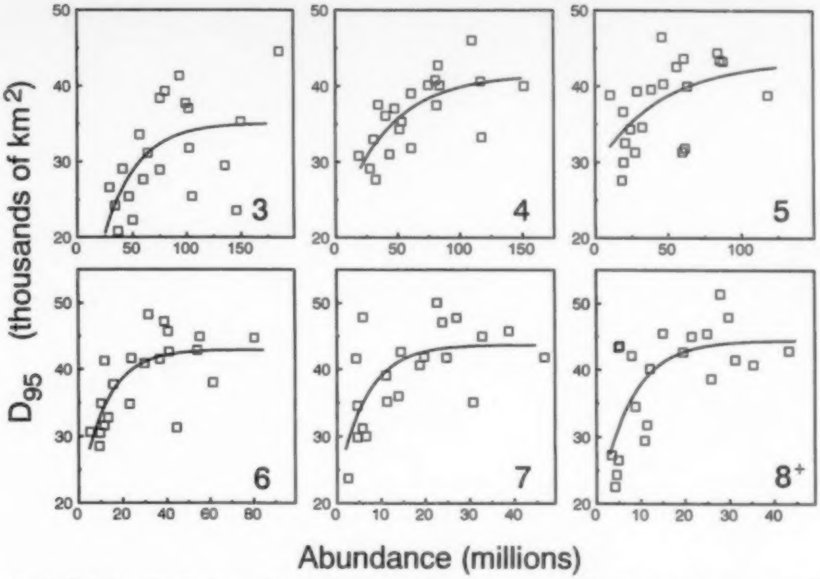

FIG. 7. Relationship between the distribution index D_{95} and abundance for age groups $3-8^+$. D_{95} is the area over which 95% of cod are distributed. The line is the predicted relationship given the model in equation 12. Parameter values and measures of goodness-of-fit are given in Table 2.

TABLE 2. Parameter estimates for the asymptotic relationship between distributional index D_{95} (thousands of square kilometres) and abundance (millions of fish) for age-classes $3-8^+$ of cod in the southern Gulf of St. Lawrence. Parameters are from equation 12 in the text. F is the ratio of explained to residual MS (df = 2,18). R^2 is the coefficient of determination. R^2_{adj} and linR^2_{adj} are adjusted coefficients of determination for the asymptotic and simple linear models, respectively. $^*P < 0.05$; $^{**}P < 0.01$.

Age	β_0	β_1	β_2	F	R^2	R^2_{adj}	linR^2_{adj}
3	35.102	33.140	0.03294	4.304*	0.32	0.25	0.22
4	41.534	20.312	0.02485	9.707**	0.52	0.47	0.39
5	43.446	14.312	0.02223	3.951*	0.31	0.23	0.23
6	42.943	22.646	0.08354	9.844**	0.52	0.47	0.33
7	43.725	21.202	0.15134	6.951**	0.44	0.37	0.26
8^+	44.479	25.641	0.13580	8.277**	0.48	0.42	0.33

D_{75} and D_{50} also tended to be positively correlated with abundance. At the single-test level, most correlations with D_{75} were significant for ages 3–5 and 8^+ whereas correlations with D_{50} were significant for age 3 only. However, with one exception (D_{75} with NT for age 4), none of these correlations were significant according to Bonferroni comparisons. Nonetheless, for age-3 cod, the correlation between D_{50} and abundance (N_3) was as strong and as significant at the single-test level as were the age-3 correlations between D_{95} or D_{90} and abundance. These results indicate that, except possibly for age-3 cod, there was no strong tendency for the area where cod densities are high to spread out as abundance increased (Fig. 8).

Discussion

We have examined three simple models of commercial fishing behaviour that span the range of possible co-distribution between fish and fishing effort. Changes in spatial spread strongly affected catchability in all three models: a fourfold increase in spread decreased catchability by 65% (model I) to 75% (models II and III). On the other hand, spatially uniform changes in abundance affected catchability only in the extreme case where fishing effort was distributed at random over all areas with fish density exceeding some minimum level (model I). Even in this extreme case, effects on catchability were relatively slight: a fourfold increase in abundance decreased catchability by only 20–30%. We consider this extreme case to be unlikely (see below) and conclude that indices of stock area or distribution that depend only on spatial spread should be better predictors of variation in catchability to commercial fisheries than indices that are affected by overall abundance.

We describe here one index of distribution that depends only on spatial spread: the minimum area over which a specified percentage of the population is distributed. For cod in the southern Gulf of St. Lawrence, the density dependence of this index depended on the percentage of the population

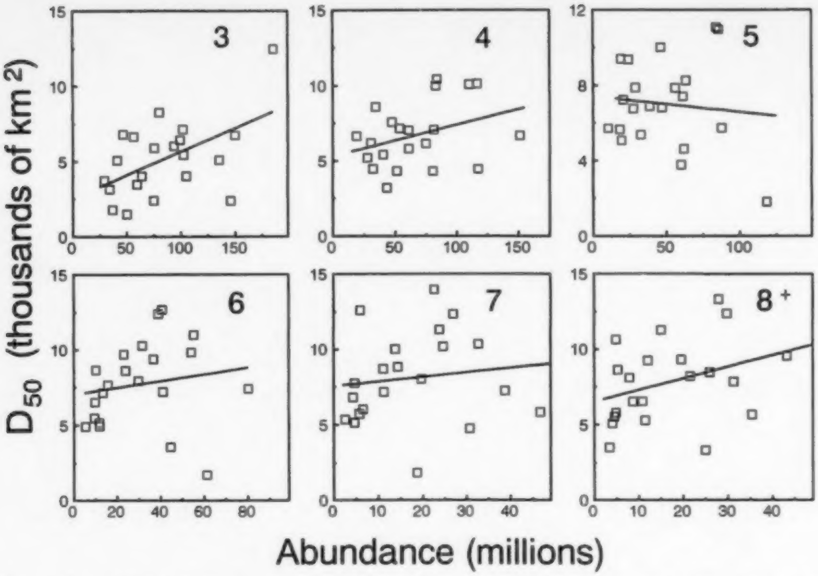

FIG. 8. Relationship between the distribution index D_{50} and abundance for age groups 3–8$^+$. D_{50} is the area over which 50% of cod are distributed. The line is the predicted linear relationship. Slope is significantly different from zero only for age group 3 (Table 1).

for which it was evaluated. The area containing most (90 or 95%) of the population was density dependent, expanding as population size increased. However, with the possible exception of age-3 cod (which are not targetted by fishermen), the area of highest cod concentration (i.e., the area containing 50% of the population) did not expand significantly as population size increased. Thus, the extent to which catchability of cod is predicted to be density dependent in the southern Gulf in September (the time of year to which our measures of fish distribution apply) will depend on fishing behaviour. If fishermen behave as in our model III, concentrating all effort in the areas of highest fish density, then catchability is predicted to be density independent. If they behave as in our model II, distributing effort over the whole stock area in proportion to local fish density, then catchability is predicted to be density dependent.

These results highlight the need for a better understanding of the distribution of fishing effort in relation to the distribution of fish. Optimal foraging theories provide a useful framework for examining fishing behaviour (Gillis et al. 1993; see Rosenzweig 1985 for a review). If fishermen act like "ideal free" foragers (i.e., have perfect knowledge of resource distributions and have free access to all sites; Fretwell and Lucas 1970; Fretwell 1972), then they should occupy only the most suitable sites when effort is low relative to fish abundance (i.e., when there is no competition among fishing vessels). This behaviour is assumed in our model III. As effort increases, then suitability of the "best" sites will decline due to competition until previously less suitable sites become equally attractive and are fished. In this case, if fishing success is inversely proportional to effort in an area (cf. the "input matching" rule, Parker 1978) and fishermen have equal competitive abilities, then effort should match fish density. This is the behaviour assumed in our model II. When fishermen differ in competitive ability, then overuse of poor patches is likely (Houston and McNamara 1988).

Recent studies have tested some of the assumptions and predictions of these "ideal free" models. These studies have provided evidence for competition among fishing vessels (Abrahams and Healey 1993; Gillis et al. 1993) and variation in competitive ability (Hilborn 1985; Abrahams and Healey 1990). Gillis et al. (1993) reported evidence that catch rates may be equalized among areas fished because of the movement of boats among areas (as predicted by ideal free models). Hilborn and Ledbetter (1979) documented vessel movements among areas in response to local changes in catch rate but found that catch rate was not equalized among areas, possibly due to variation in factors such as operating costs and fishing conditions. Hilborn and Ledbetter (1979) and Hilborn (1985) also presented evidence that effort by some fleet sectors is limited to occasional exploratory trips when catch rates drop below some minimum threshold (presumably set by marginal costs such as operating expenses and alternative opportunities). These studies suggest fishing behaviour intermediate between those assumed in our models I and II, with (1) effort distributed over a range of fish densities and (2) effort tending to be greater in areas with greater fish densities but (3) an overuse of areas with lower fish densities. Few studies have directly compared the distributions of fish and fishing effort. An exception is the study of Rose and Leggett (1993). They found that fishing effort closely tracked general seasonal trends in fish distribution but that fishermen were less successful in tracking higher frequency day to day variation in fish distribution. We concur with Hilborn (1985) that there is an urgent need for more such studies of fishery dynamics.

The index of distribution described here can be used when data are collected using a spatially stratified survey design, a design typically employed in fisheries research surveys. When data are collected using other designs, analogous indices that depend only on spatial spread could be constructed using geostatistical or other mapping techniques (see Simard et al. 1992 and Petitgas 1993 for applications of geostatistics to fisheries and marine ecology). This would involve estimating abundance within contours of progressively lower density until a specified percentage of the population was estimated. The area within the contours enclosing this percentage of the population would be the index of distribution. Alternative indices of the type described by Murawski and Finn (1988) and Marshall and Frank (1994) could also be constructed. These indices are based on the distances between sample sites and the center of fish distribution or some fixed reference point. Indices that are independent of overall abundance could be constructed by weighting each distance by the proportion of the total survey catch caught at that site. However, indices of this type do not depend only on spatial spread. Indices that use a fixed reference point confound changes in spread and changes in the center of distribution. Density-dependent shifts in the center of distribution (i.e., in the region where cod are most concentrated) have recently been demonstrated for Atlantic cod (Swain and Wade 1993). For this reason, we do not recommend indices based on a fixed reference point. Indices that use the center of distribution may confound changes in spread and changes in modality (i.e., unimodal versus multimodal distributions). This could be a particular problem when a population is composed of spatially discrete substocks or is distributed among several separate geographic regions. In these cases, the calculated "center" of distribution may be a region unoccupied by the population. For these reasons, we believe that indices of the type described here, which depend only on the area over which a specified percentage of the population is spread, should be used if the aim is to examine effects of variation in fish distribution on catchability to commercial fisheries.

As expected, the indices of distribution used in this study were not as closely correlated with abundance as were stock areas defined in terms of constant density thresholds. Variation in abundance explained 63–94% of the variation in stock area of cod in the southern Gulf when stock area was defined as the area over which estimated density exceeded a constant threshold (Swain and Wade 1993). However, using the same model (equation 12), variation in abundance explained only 31–52% of the variation in the area containing 95% of cod in the southern Gulf (Table 2). This difference could be partly due to differences between the two studies in abundance estimates (the previous study did not include data from recent years and used a different method to calibrate sequential population analysis) or in statistical approach (i.e., geostatistical versus design based). However, using the abundance estimates from this study and a design-based method (i.e., equations 10 and 11) to estimate the area over which density exceeded the constant thresholds used in the previous study, coefficients of determination were only slightly lower (47–93%) than in the previous study. Thus, when stock area is defined in terms of constant density thresholds, the density dependence of stock area may overestimate the density dependence of catchability.

Previous studies have nevertheless demonstrated an inverse relationship between catchability and stock area, where stock area is defined as the area over which density exceeds some constant threshold of abundance (Crecco and Overholtz 1990; Rose and Leggett 1991). The variation in stock area reported in these previous studies appears to reflect variation in spatial spread rather than spatially uniform variation in abundance. In both studies, stock area increased at about the same rate as abundance (i.e., a fivefold increase in biomass was associated with a fivefold increase in stock area). Considerably smaller changes in stock area are expected if changes in abundance are spatially uniform (Fig. 2). Rose and Leggett (1991) also reported that local density maxima were relatively constant, indicating an increase in spatial spread as cod abundance increased (see also Crecco and Overholtz 1990). Similarly, Swain and Wade (1993) showed that cod density did *not* increase uniformly over all areas as population size increased. For younger cod (age 3), this regional variation in the rate of density change appeared to reflect an increase in spatial spread as abundance increased. However, for older cod (ages $4–8^+$), shifts in the "center" of distribution also contributed to this regional variation in rates of density change (see fig. 7 in Swain and Wade 1993). The index of distribution used in this study disentangles these two sources of variation in rates of local density change and confirms that spatial spread increased (i.e., the area containing most of the population expanded) as abundance increased for all ages ($3–8^+$) of cod.

The area of highest cod concentration expanded significantly as population size increased for young (age-3) cod but not for older cod. One interpretation of this difference could be that spatial pattern is more sensitive to variation in abundance for young cod than for older cod. However, analyses of regional variation in cod density suggest the opposite (Swain and Wade 1993). As population size increased, density increased slowly in regions where cod were most abundant at low population sizes and more rapidly in surrounding areas. For young cod, this resulted in an increase in the number of regions where cod densities were relatively high (i.e., the area of highest cod concentration expanded). For older cod, density increased even more rapidly in the surrounding areas, so that the area of highest densities actually shifted from the region preferred at low abundance to adjoining regions at high abundance. Thus, as abundance increased, spatial pattern changed more dramatically for older cod, even though this was not reflected in an expansion of the area of highest cod concentration. Possible reasons for this difference between age groups in spatial response to abundance are discussed in Swain and Wade (1993). These results emphasize that no single statistic is likely to provide a complete picture of spatial responses to variation in abundance (see also Marshall and Frank 1994).

Acknowledgements

We thank G.A. Rose for helpful comments on this work.

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Phosphorus Fluxes in Limnetic Cladocerans: Coupling of Allometry and Compartmental Analysis[1]

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Wen, Y.H., A. Vézina, and R.H. Peters. 1994. Phosphorus fluxes in limnetic cladocerans: coupling of allometry and compartmental analysis. Can. J. Fish. Aquat. Sci. 51: 1055–1064.

A size-dependent two-compartment model was developed for estimation of ^{32}P turnover and fluxes by limnetic cladocerans in steady state. After feeding on radioactively labelled food, uniformly labelled animals were fed unlabelled cells and the time course of release of tracer followed. Rates of turnover and size-specific fluxes were subsequently fitted to a two-compartment model. The model predicted that steady-state turnover and size-specific fluxes for ^{32}P excretion declined with body weight and that the exponent of weight did not significantly differ from −0.25, suggesting the relationships between total P turnover or flux rates and body size in cladocerans follow the same allometry observed for other organisms and other metabolic activities. However, rate constants for intercompartmental exchanges declined faster than weight$^{-0.25}$, indicating that their turnover and flux declined much faster with increasing body size than would be expected from general allometry. Size-specific ingestion and assimilation rates of ^{32}P by cladocerans decreased with increasing body size with a slope of the allometric function similar to −0.25.

On a créé un modèle à deux compartiments et qui est fonction de la taille pour estimer le flux et le turnover du ^{32}P à l'état constant chez des cladocères limnétiques. Après avoir été nourris avec des aliments marqués radioactivement, des animaux uniformément marqués ont été nourris de cellules non marquées et on a mesuré l'évolution dans le temps de la remise en circulation du marqueur. Le turnover et le flux en fonction de la taille ont subséquemment été ajustés à un modèle à deux compartiments. Le modèle prévoit que le turnover et que les flux stables en fonction de la taille, dans le cas de l'excrétion du ^{32}P, diminuent en fonction de la masse corporelle et que l'exposant affecté à la masse ne diffère pas significativement de −0,25; cela laisse présumer que les rapports entre le turnover total ou le flux de P et la masse corporelle des cladocères suivent la même allométrie qui est observée chez d'autres organismes et pour d'autres activités métaboliques. Cependant, les constantes de vitesse des échanges entre compartiments diminuent plus rapidement que la valeur de la masse corporelle$^{-0,25}$; cela indique que le turnover et le flux diminuent beaucoup plus rapidement, avec l'augmentation de la masse corporelle, que ce que permettrait de prévoir l'allométrie générale. Les taux d'ingestion et d'assimilation en fonction de groupes de taille précis du ^{32}P par des cladocères diminuent à mesure qu'augmente la masse corporelle, avec une pente décrivant la fonction allométrique qui est semblable à −0,25.

Received August 6, 1993
Accepted November 26, 1993
(JC040)

Reçu le 6 août 1993
Accepté le 26 novembre 1993

The need for a realistic, general model to quantify phosphorus (P) fluxes in zooplankton has often been stressed (Rigler 1973; Vézina 1986) and several models have been proposed for various zooplankton species (Peters and Rigler 1973; Peters 1975; Taylor and Lean 1981; Taylor 1984). These studies have found applications in simulation models of nutrient regeneration (Ikeda et al. 1982; Ejsmont-Karabin 1984; Olsen and Østgaard 1985), in comparing the role of P cycling by different organisms (Ganf and Blazka 1974; Nakashima and Leggett 1980; James and Salonen 1991), and in describing P fluxes through living organisms (Lehman 1980; den Oude and Gulati 1988). However, the formulation of a more general model has been hindered by the limited flux data for many species.

One limitation of existing models is their inability to predict the dynamics of P turnover and flux in aquatic animals. Although radiotracer techniques have been used to study the P cycle in aquatic ecosystems for decades, there has been little use of compartmental kinetics to analyze P turnover and fluxes. The rather comprehensive model of Peters and Rigler (1973) is essentially a one-compartment analysis of internal tracer loss. Shipley and Clark (1972), Conover and Francis (1973), and Lampert and Gabriel (1984) cautioned that considering an animal as a single, instantaneously mixed compartment might cause considerable errors in assessment of material flow in biological systems. Perhaps for this reason, the Peters and Rigler model overestimates P excretion rates for small animals (Peters and Rigler 1973) and in oligotrophic waters (Olson and Østgaard 1985). Moreover, although the Peters and Rigler model incorporated the effects of temperature, food level, and body size on P release, it was generated from data for only a single species, *Daphnia rosea*, and therefore covered a limited size range. Perhaps because of these restrictions, its description of the effect of size on excretion rate is anomalous: instead of the expected

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TABLE 1. List of major symbols used and their meanings and dimensions.

Symbol	Parameter description
A	Assimilation, $\mu g \cdot mg^{-1} \cdot h^{-1}$
A_a, A_b	Coefficients (intercepts) in double exponential expansion, CPM·min^{-1}
AE	Assimilation efficiency, dimensionless
b	Exponent in allometric equations, dimensionless
F_{ab}, F_{ba}	Flux rates of P from pool *b* to pool *a* and from pool *a* to pool *b*, $\mu g \cdot mg^{-1} \cdot h^{-1}$
F_{ao}	Rate of transfer of P from environment to compartment *a*, $\mu g \cdot mg^{-1} \cdot h^{-1}$
F_{oa}	Rate of transfer of P from compartment *a* to the environment, $\mu g \cdot mg^{-1} \cdot h^{-1}$
I	Ingestion rate, $\mu g \cdot mg^{-1} \cdot h^{-1}$
k_a, k_b	Fractional turnover rate of P transfer from compartments *a* and *b*, min^{-1}
k_{ab}, k_{ba}, k_{oa}	Fractional turnover rate of P from compartment *b* to compartment *a*, from compartment *a* to compartment *b*, and from compartment *a* to the environment, min^{-1}
Q_a, Q_b	Pool size of compartments *a* and *b*, μg
W	Animal body dry weight, mg

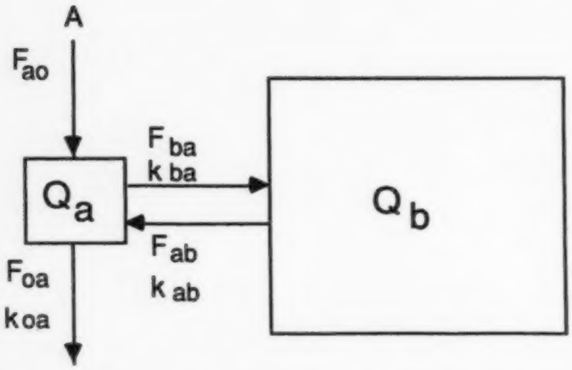

FIG. 1. Diagrammatic representation of the two-compartment model of ^{32}P kinetics in cladocerans. ^{32}P is introduced to the metabolic compartment (Q_a) through the animal's diet at a constant rate F_{ao}. ^{32}P accumulating in the structural compartment (Q_b) is described by a rate constant (k_{ba}) or a rate F_{ba}. Through recycling, ^{32}P returns from Q_b to Q_a with a rate constant of k_{ab} or a flux rate F_{ab}. A certain amount of ^{32}P is removed from Q_a through excretion with a rate constant (k_{oa}) or a rate of F_{oa}.

body weight exponent of −0.25 (Peters 1983), the allometric slope was −0.38, which suggests that size-specific excretion rates fall much more rapidly with size than expected. This model needs further development and refinement.

Lampert and Gabriel (1984) suggested that a two-compartment, open, reversible system is a more appropriate model of ^{14}C dynamics in *Daphnia*. In the present paper, we extend this model to treat P turnover and fluxes in limnetic cladocerans of different size. The model parameters were determined by laboratory studies of ^{32}P kinetics and analyzed by both compartmental modelling and allometric parameterization. We further tested an a priori expectation that the exponents of the allometric equations relating P fluxes to body size should approximate −0.25 (Peters 1983). Our general premise is that all processes of material fluxes in aquatic organisms can be fitted to a single model, provided that the model's fundamental parameters can be described as functions of characteristics of the organisms, especially body size, and their environment, such as food level and water temperature.

Two-Compartment Model

The conceptual model (Fig. 1, symbols and abbreviations as in Table 1) is a slight modification of the two-compartment configuration used by Lampert (1975) and Lampert and Gabriel (1984) to quantify ^{14}C turnover in *Daphnia*. In the model, ^{32}P is conceptualized to be distributed between two kinetically, but not necessarily anatomically, identifiable compartments inside the animal: a small, rapidly turning over "metabolic" compartment or pool (Q_a) and a large, slowly turning over "structural" pool (Q_b). We assumed that ^{32}P enters the metabolic pool by assimilation through the gut and that irreversible P loss occurs from the metabolic pool through excretion. The two pools are open in the sense that Q_a interchanges with Q_b. The rates of change of ^{32}P in each pool were established by algebraic summation of rates of acquisition and loss of tracer, which is mathematically described for pool *a* as

$$(1) \qquad dQ_a/dt = F_{ao} + F_{ab} - F_{ba} - F_{oa} = F_{ao} + k_{ab}Q_b - Q_a(k_{ba} + k_{oa})$$

and for pool *b* as

$$(2) \qquad dQ_b/dt = F_{ba} - F_{ab} = k_{ba}Q_a - k_{ab}Q_b.$$

At apparent dynamic equilibrium,

$$(3) \qquad dQ_a/dt = dQ_b/dt = 0.$$

The rate constants (k_{ab}, k_{ba}, k_{oa}) were calculated by numerical integration of simultaneous differential equations (1) and (2) and fitted to time courses of ^{32}P release.

In the modelling processes, we further specified that the rate constants (k) and flux parameters (F_{ab}, F_{ba}, F_{oa}) are power functions of body size (W) such that

$$(4) \qquad \text{Rate parameters } (k \text{ or } F) = aW^b.$$

In all cases, flux rates represent mass specific fluxes and have the units micrograms of P per milligram per hour.

Materials and Methods

Animal Culture, Sizing, and Body P Determinations

Six species of cladocerans (*Daphnia magna*, *D. pulex*, *D. galeata*, *Simocephalus vetulus*, *Ceriodaphnia quadrangula*, and *Bosmina longirostris*) were kept in separate aquaria with dechlorinated Montreal tap water on a 14 h light : 10 h dark cycle. The water temperature was maintained at approximately 20°C. Stock animals were fed ad libitum with "green water" from a goldfish tank (Peters 1987a). The animals used in the experiments were sized under a dissecting microscope fitted with an ocular micrometer. Length (L, millimetres) was taken as the distance from the anterior margin of the head to the base of the tail spine. Dry body weight (W, milligrams) of the large species was obtained by drying 10–25 sorted animals of different sizes at 60°C for 24 h, cooling them in a desiccator, and weighing them individually to the nearest 0.1 μg on a Cahn Electro balance. The dry body weight of small individuals was determined for each species by weighing a group of similarly sized animals (within 0.01 mm). Animal body P content was measured with the ascorbic acid modification of the molybdenum blue technique (Strickland and Parsons 1968), after persulfate oxidation of the organically bound P (Menzel and Corwin 1965). All measurements of body P were made in duplicate.

Radioactivity Counting

Cerenkov counting was used to measure total radioactivity of the samples. Because this counting is conducted without scintillation fluor (Wang et al. 1975; Haney et al. 1986), the technique has the advantage of rapid sample preparation, reduced cost, and reduced chemical quenching. Before counting, animals were digested overnight in a tissue solubilizer at 60°C and then transferred to plastic scintillation vials. Counts were made with an LKB Wallac liquid scintillation counter for 10 min. All samples were counted in triplicate to a reliable error (95% confidence level) of ±5%. In sample preparation, all glassware and plasticware was soaked in acid overnight to remove all radioactivity, washed with P-free detergent, and rinsed three times with deionized, distilled water. All solutions were prepared with deionized, distilled water. All reagents were of reagent grade or better and checked for possible P contamination.

Isotope Labelling of Yeast

Log-phase yeast (*Rhodotorula glutinis*) grown in Downing and Peters' (1980) culture medium was placed in carrier-free medium containing approximately 50 kBq of $[^{32}P]PO_4$ (New England Nuclear) and incubated at room temperature for over 24 h to incorporate the tracer. During exposure, the uniformity of labelling of the yeast was checked by comparing the specific activity of a labile cell fraction with that of the whole cells. The labile cell fraction was obtained by centrifuging the labelling yeast cells, resuspending them in 100 mL of ice-cold 10% (w/w) trichloroacetic acid (TCA) for 10 min, and centrifuging them again to collect the supernatant. Samples of the supernatant and whole radioactive culture were then assayed for radioactivity by a liquid scintillation counter in five replicates; other subsamples were chemically analyzed for total P.

P Ingestion

We determined the ingestion rates of ^{32}P-labelled yeast cells by different sized cladocerans with the technique of Rigler (1971). From 50 to 300 animals, depending on size, were allowed to feed for 30–60 min in a feeding chamber containing 500–1000 mL of nonradioactive yeast suspension at a concentration of 10^5 cells·mL^{-1}. Burns and Rigler (1967) indicated that *Daphnia* reached maximum feeding rates at this concentration. McMahon (1965) and Geller (1975) reported that a prefeeding time of 30 min was needed for adaptation to food concentration and quality. The feeding period before labelling also allowed animals to acclimatize to the test conditions and minimized differences in initial gut fullness. After the initial feeding period, an equal volume of ^{32}P-labelled yeast suspension at the same concentration as the nonradioactive cells was added to the chamber and gently mixed with the nonradioactive suspension. At 2- to 15-min intervals, three to five individual animals were quickly removed from the feeding chamber, anaesthetized in carbonated water, rinsed thoroughly in distilled water, transferred to plastic scintillation vials, and immediately measured for radioactivity. Uptake curves were established by plotting radioactivity in animals as a function of feeding time. To delimit the ingestion phase in the uptake curves, we applied the STEPWISE procedure (SAS Institute Inc. 1983) to fit the data to the quadratic regression

$$(5) \qquad y = a_1 + b_1x + b_2x^2$$

where y is animal body radioactivity and x is feeding time. The first inflection point was taken to indicate the onset of defecation of unassimilated tracer. Since in the initial stage of the radioactive feeding, the radioactivity of the animal body should increase linearly with time (Rigler 1971), we expected that the slope (b_1) of the linear term (x) would be significantly different from 0, but the slope (b_2) of the quadratic term (x^2) would be not significant. We tested this a priori expectation by adding each time point sequentially to the regression equation until b_2 became significant, which indicates a curvilinear change resulting from egestion of radioactive food (Rigler 1971). The linear slope (b_1) was taken as tracer uptake rate (CPM per milligram per minute) and converted to P ingestion rates (micrograms per milligram per minute) on multiplication by the specific activity (CPM per migrogram of P) of the yeast P.

P Release

Isotope release measurements were performed in 21-mL gel-filtration columns (Pharmacia Fine Chemicals), which had been modified to flow-through chambers by fitting each end with Pharmacia flow adapters with 75-μm Nitex screens to retain the animals in the columns. Groups of 5–25 animals of similar size, which had been fed labelled yeast cells at 10^5 cells·mL^{-1} for 7–10 d (Peters and Rigler 1973), were gently introduced to the column to allow adaptation to the experimental conditions. A suspension of 10^5 radioactive yeast cells·mL^{-1} was pumped into the top of each column by a Buchler peristaltic pump at 1 mL·min^{-1}. After 30–60 min, an identical concentration of nonradioactive yeast culture was pumped in at 5 mL·min^{-1} for 5 min to replace all radioactive suspension in the column and to allow animals to begin to clear their guts of undigested radioactive cells. Because flow is laminar in these columns, 5 min was sufficient to flush the entire column, as confirmed by experiments with dye. The flow rates were then reduced to 1 mL·min^{-1}, the eluant was collected at 5-min intervals for 8–24 h by an LKB automatic fraction collector, and the radioactivity of subsamples of each fraction was determined.

^{32}P release rate was estimated from the time course of radioactivity in the eluant. Since samples collected in the first 5–15 min were likely contaminated by radioactive feces, depending on body size, the first 5- to 15-min samples were

TABLE 2. Time course of specific activity of TCA extractable fraction (TCSA, CPM), total specific activity of the yeast suspension (TSA, CPM), TCSA/TSA (%), total P (μg), and total radioactivity (TA, CPM) of the yeast cells ($n = 5$).

Labelling time (h)	TCSA		TSA			Total P		TA	
	Mean	SD	Mean	SD	%	Mean	SD	Mean	SD
48	0.298	0.026	0.319	0.028	93.23	0.186	0.006	53 161	3783
72	0.324	0.010	0.328	0.021	98.81	0.184	0.004	54 080	2886
96	0.301	0.008	0.299	0.011	100.64	0.188	0.003	50 217	1473

discarded in the estimation. As a result, ^{32}P release is intended to represent excretion only. To determine the ^{32}P turnover rate constant in each fully labelled compartment over time, we first fitted the tracer data to a double exponential function:

(6) $A_t = A_a\exp(-k_a t) + A_b\exp(-k_b t)$.

All curve fitting was conducted by the 3R routine of the BMDP package. This program allows direct iterative estimation of nonlinear parameters using the efficient algorithm of the Newton–Raphson procedure (Dixon 1988). The adequacy of the model fit was assessed by the residual sum of squares (RSS), the asymptotic standard deviations of the parameters, and the homoscedasticity of the residuals with time. This approach to fitting compartmental models is much more direct, convenient, and powerful than the traditional curve peeling of the graphical method (Riggs 1963). Estimates for the components (k and A) of experimental decay curves emerge directly from the Newton–Raphson fitting procedure, so there is no need to subtract the asymptote from the curve (Conover and Francis 1973). The computer program provides the asymptotic standard deviation, which is essential for statistical comparisons.

We used both fractional turnover and P flux to represent ^{32}P loss from a pool. Fractional rate of loss is calculated as a proportion of the P content of the pool lost per unit of time and is expressed per minute. For P flux, the loss was expressed in absolute units (micrograms per minute). The two rates are related by

(7) Fractional turnover rate = P flux rate/P content of the pool.

The fractional rates of turnover from pool a to pool b (k_{ba}) and from the metabolic pool to the outside (k_{oa}) were estimated after normalization of equation (6) using the techniques described by Shipley and Clark (1972). Because the intercompartmental turnover rate (k_{ab}) cannot be determined accurately, it was calculated by solving the differential equation (2) at steady state:

(8) $k_{ab} = k_{ba} \times Q_a/Q_b$.

The relative pool sizes of compartments Q_a and Q_b were computed from the exponents and time-zero intercepts of the double exponential expression of ^{32}P loss (equation (6)) by the method of Conover (1961). The absolute sizes of each pool were then calculated by multiplying the total body P content by the relative pool size. P flux was estimated as the product of the absolute pool size of the donor pool and its corresponding fractional turnover rate.

P Assimilation

To explore P metabolism in cladocerans further, we estimated ^{32}P assimilation rates as model-derived influx rates (F_{ao}). For comparison with the rates of ^{32}P assimilation, ^{32}P ingestion rates for these experimental animals were calculated from the experimentally determined size-specific ingestion rate functions. Assimilation efficiency was then calculated as assimilation rates/ingestion rates × 100 (Peters 1984). Both assimilation rates and efficiencies were analyzed as a function of size.

Allometric Statistics

We estimated the slopes and intercepts of all allometric relationships by least-squares linear regression of log-transformed data. The strengths of the relationships were determined by the coefficients of determination (r^2), standard errors of the regression ($S_{y.x}$), and by visual inspection of the data plots. The homogeneity of the allometric lines was tested with an F-test and the null hypothesis ($b = -0.25$) was tested with a Student t-test. For all statistical comparisons, $p < 0.05$ was considered to represent a significant difference.

Results and Discussion

Body Dry Weight and P Content

The allometric relation between body dry weight (W, milligrams) and body length (L, millimetres) for all species studied is best described as

(9) $W = 0.013L^{2.14\pm0.12}$ ($r^2 = 0.85$, $S_{y.x} = 0.55$, $n = 54$, $p < 0.01$)

where 0.12 is the standard error of the slope. Both the allometric scaling factor (2.14) and the constant (0.013) in the above power function agree well with those reported by Burns (1969), Porter et al. (1982), and Lynch et al. (1986) for freshwater cladocerans. There is also a significant power function between dry body weight (W, milligrams) and body P content (P, micrograms), which can be quantitatively described by the equation

(10) $P = 13.18W^{1.02\pm0.03}$ ($r^2 = 0.98$, $S_{y.x} = 0.20$, $n = 28$, $p < 0.01$).

On average, individual body P content was 1.26% of its dry body weight, which is also similar to published values (Vijverberg and Frank 1976; Peters 1983; Behrendt 1990; Andersen and Henssen 1991).

Homogeneity of Yeast Labelling

^{32}P incorporation by the yeast cells reached an equilibrium about 72 h after inoculation (Table 2). The efficiency of label uptake became highest on the third and fourth day of culture, when 98–100% of ^{32}P was bound in yeast cells.

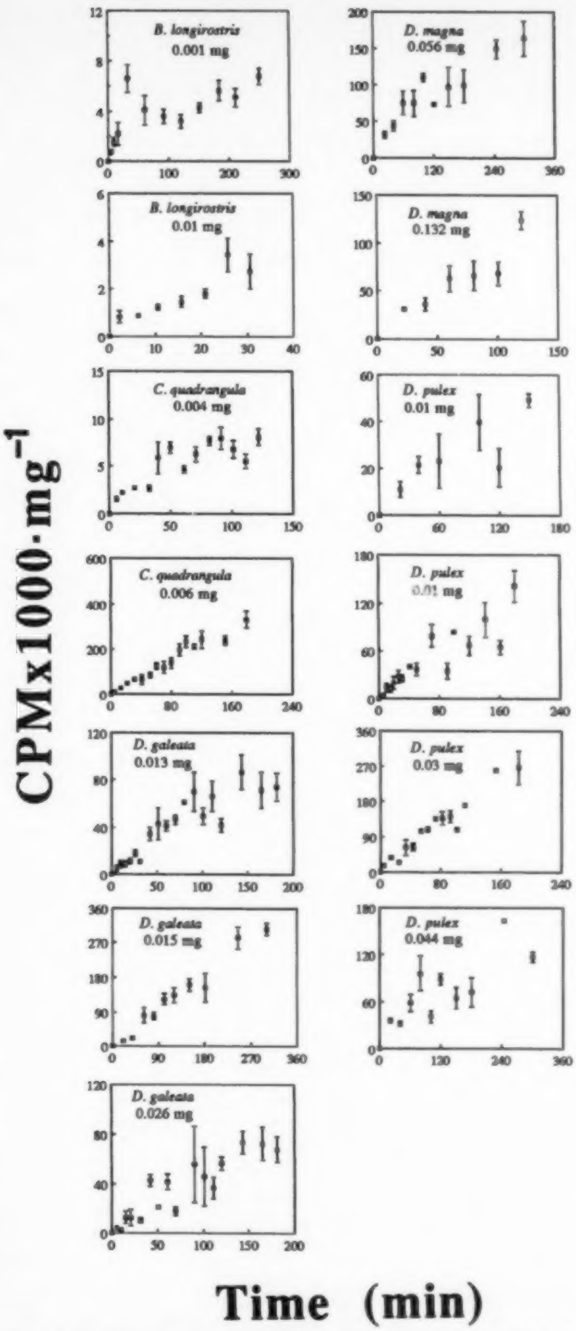

FIG. 2. Changes (mean ± SD) of body ^{32}P activity in individual groups of cladocerans after transfer from nonradioactive to radioactive yeast suspension.

There was no significant difference in radioactivity between these two days (t-test, $n = 5$, $p > 0.05$), indicating that 3–4 d was long enough to achieve homogeneous labelling, which is consistent with the yeast labelling time of other studies (Peters and Rigler 1973). After 96-h radiolabelling, 2.7×10^5 CPM was equivalent to 1 μg of the yeast TP.

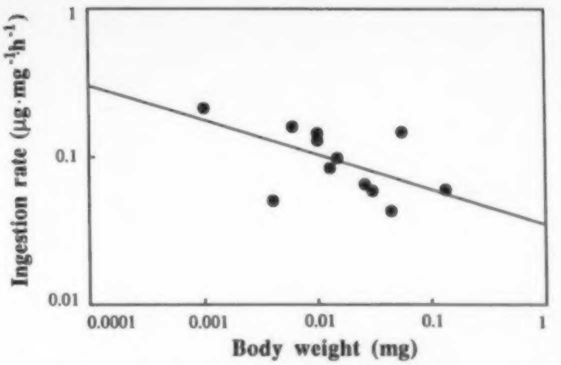

FIG. 3. Allometric relations describing the size dependence of P ingestion rate in cladocerans feeding on a radiolabelled yeast suspension.

P Ingestion

The time course uptake of ^{32}P from labelled yeast cells by cladocerans differed considerably among species (Fig. 2). Nevertheless, in all species, the uptake of radioactivity was almost linear over the first 5–60 min after introduction of the radioactive food suspension. This may reflect constant rates of feeding as the animals consumed radioactive food. Thereafter, the rates of accumulation became less rapid, probably reflecting the simultaneous processes of defecation and excretion. There are no clear inflection points in the uptake curves, so gut passage time could not be estimated adequately. A similar difficulty was encountered by Muck and Lampert (1984) in their studies of *Daphnia* feeding on ^{14}C-labelled algae. This gradual transition between ingestion and assimilation may be attributed primarily to the interindividual variability in feeding activity and assimilation efficiency and to high assimilation efficiency when cladocerans eat P-limited food (Olsen and Østgaad 1985).

Although highly variable, size-specific P ingestion rates (I, micrograms per milligram per hour) show a strong tendency to decrease with increasing body size (Fig. 3) and can be described by the following power model:

$$(11) \quad I = 0.035W^{-0.24(\pm 0.09)} \; (r^2 = 0.39,\ S_{y,x} = 0.19,\ n = 13,\ p < 0.01).$$

The exponent of -0.24 is not significantly different from -0.25 (t-test, $p > 0.05$), implying that the ingestion rates have the same body size dependence as other metabolic rates for other animals (Peters 1983).

P Release

^{32}P activity of cladoceran excreta declined rapidly when the animals were placed in unlabelled yeast suspension. The initial 5- to 15-min changes were excluded, since they included the defecated label. The subsequent loss of radioactivity was exponential (Fig. 4). In 1–5 min, the excreta radioactivities were reduced to 20–30% of the initial values. Thereafter, changes in release rates of the isotope became gradually smaller and more linear. There was pronounced variability in the release curves both among individuals (Fig. 4) and among species (Table 3). This variation is common in labelled excretion experiments (Marshall and Orr 1955) and probably reflects experimental stresses on the animals.

TABLE 3. Values (mean ± SD) of model parameters deduced from computer-curve fitting a double exponential equation to excreted ^{32}P activity data and the relative pool sizes of two compartments in the different species of cladocerans studied. N is the number of runs.

Species	N	Mean dry weight (mg)	A_a (CPM·min^{-1})	k_a (min^{-1})	A_b (CPM·min^{-1})	k_b (min^{-1})	% Q_a	% Q_b
D. magna	1	0.2	570.79	0.0167	767.67	0.0010	4.35	95.65
S. vetulus	1	0.05	55.38	0.0358	280.21	0.0021	1.24	98.86
D. galeata	3	0.027 ± 0.009	363.64 ± 185.00	0.0482 ± 0.0197	621.50 ± 218.82	0.0019 ± 0.0010	2.18 ± 0.51	97.82 ± 0.51
D. pulex	4	0.054 ± 0.035	377.72 ± 233.55	0.0495 ± 0.0318	292.47 ± 166.00	0.0011 ± 0.0005	3.28 ± 1.44	96.72 ± 1.44
C. quadrangula	5	0.007 ± 0.003	197.81 ± 115.77	0.0911 ± 0.0082	159.57 ± 197.58	0.0029 ± 0.0024	3.26 ± 0.93	96.74 ± 0.93

Based on the fit to the data, for most experiments, ^{32}P activity–time relations conformed to a simple two-compartment model (Fig. 4). For others (mainly *D. magna*, and some *C. quadrangula* and *D. pulex*), a higher order compartmental model seems to fit better. The coefficients (time zero intercept) and exponents (fractional rate constants) of the exponential function fitted to all curves for ^{32}P loss (Table 3) showed significant variations among different sizes and species of cladocerans. The fractional turnover rates of pool a (k_a) varied sixfold and those of pool b (k_b) varied 21-fold. There was a clear trend for small individuals to have large fractional turnover rates for pool a ($b = -0.46$, $r^2 = 0.73$, $S_{y,x} = 0.16$, $n = 14$, $p < 0.01$). There was a similar trend for pool b, but the power function was not significant ($b = -0.27$, $r^2 = 0.15$, $S_{y,x} = 0.36$, $n = 14$, $p > 0.05$). This lack of significance reflects the high variations of the second exponents, possibly related to the small values of the rate constants in the large compartments.

The relative pool sizes of both exchangeable compartments (%Q_a and %Q_b) varied only slightly among species (Table 3) ranging between 1 and 5% for pool a. The relative dimensions of both pools are independent of body size (for pools a and b: $r^2 = 0.06$, $S_{x,y} = 1.42$, $n = 14$, $p > 0.05$).

The values of k_{ba} were 18–87 times bigger than those of k_{ab} and both parameters varied over an order of magnitude. The fractional turnover rates for excretion were intermediate between k_{ab} and k_{ba} and varied over 10 times as well. The fractional rate constants for the conversion between two pools (k_{ab} and k_{ba}) and for the excretion from the first pool (k_{oa}) declined with increasing body size (Fig. 5) and can be described by the following power functions ($n = 14$):

$$(12) \quad k_{ab} = 0.00004W^{-0.66\pm0.26} \; (r^2 = 0.35, S_{y,x} = 0.52, p < 0.05)$$

$$(13) \quad k_{ba} = 0.0024W^{-0.54\pm0.18} \; (r^2 = 0.44, S_{y,x} = 0.35, p < 0.05)$$

$$(14) \quad k_{oa} = 0.0011W^{-0.31\pm0.08} \; (r^2 = 0.56, S_{y,x} = 0.16, p < 0.01).$$

The exponent (−0.31) for k_{oa} does not significantly differ from theoretical expectation for $b - 1 = -0.25$ (t-test, $n = 14$, $p > 0.05$). Similar exponents have been determined experimentally for many metabolic activities of zooplankton (Peters 1983, 1987b). However, the exponents of k_{ab} and k_{ba} were significantly less than expected, so these rate constants decrease much faster with body size than does excretion (t-test, $n = 14$, $p < 0.01$).

Both intercompartmental flux rates and excretion rates decreased with increasing body size (Fig. 6) and can be reflected by the following equations ($n = 14$):

$$(15) \quad F_{ba} = F_{ab} = 0.049W^{-0.52\pm0.23} \; (r^2 = 0.31, S_{y,x} = 0.46, p < 0.05)$$

$$(16) \quad F_{oa} = 0.021W^{-0.30\pm0.11} \; (r^2 = 0.28, S_{y,x} = 0.25, p < 0.05).$$

The exponent (−0.30) of the allometric equation for F_{oa} did not significantly differ from −0.25 (t-test, $n = 14$, $p > 0.05$), indicating that this flux rate followed the same trend as other physiological rates of routine metabolism with respect to relation to body size. The exponents of F_{ba} and F_{ab} are, however, significantly lower than −0.25 (t-test, $p < 0.01$), suggesting that these flux rates decrease much faster with body size than release rates.

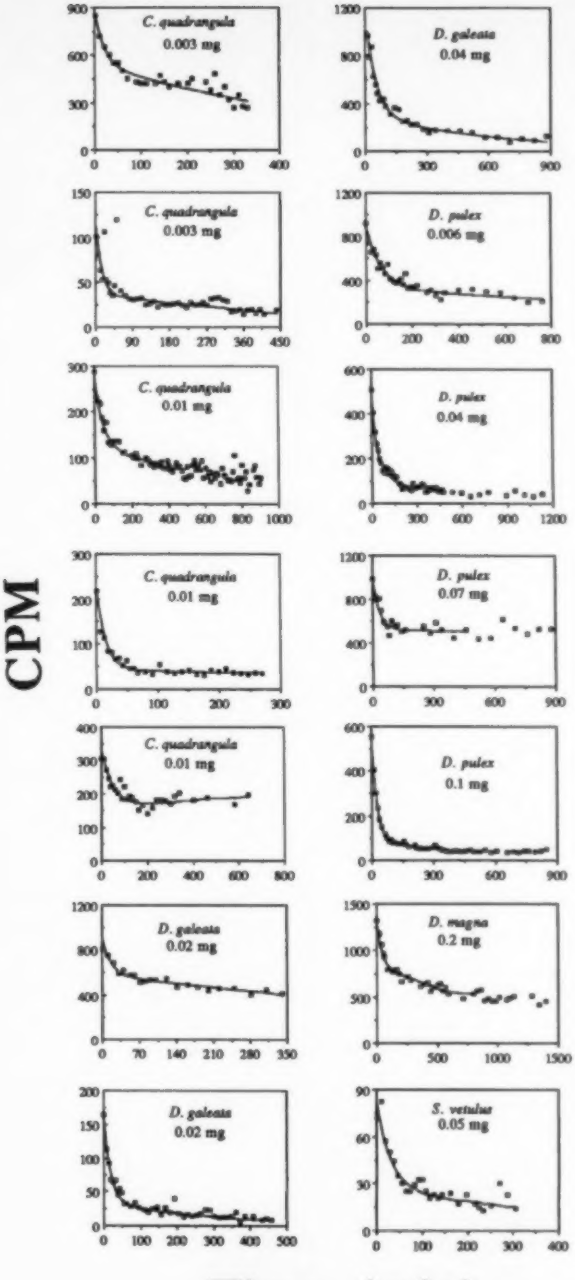

FIG. 4. Experimentally observed (points) and model-fitted (solid line) time course curves of ^{32}P excreted by initially fully labelled individual groups of cladocerans feeding on nonradioactive food at various time intervals.

P Assimilation

Our model assumes that assimilation rates (F_{ao}) are equal to excretion rate (F_{oa}) in steady state (equation (2)). The slope of the power function for ^{32}P size-specific assimilation rates would therefore be close to -0.25, as expected, and the assimilation efficiencies can be then derived by the power equation

$$(17)\quad AE = A/I = 0.021W^{-0.30}/0.035W^{-0.24} = 0.60W^{-0.06}.$$

Because the exponent (-0.06) is very close to zero, cladoceran P assimilation rates appear to be above 60% (66–85%) of ^{32}P ingestion and independent of body size.

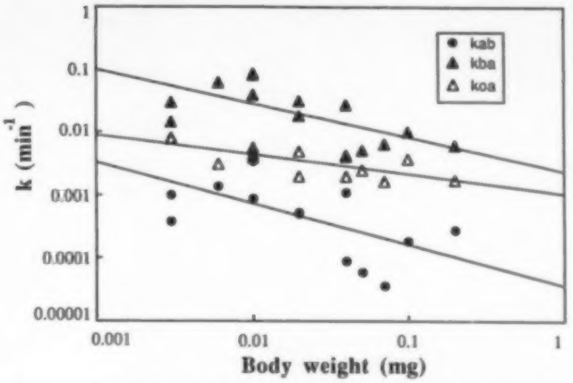

FIG. 5. Allometric relations describing the size dependence of intercompartmental release and fractional turnover rates.

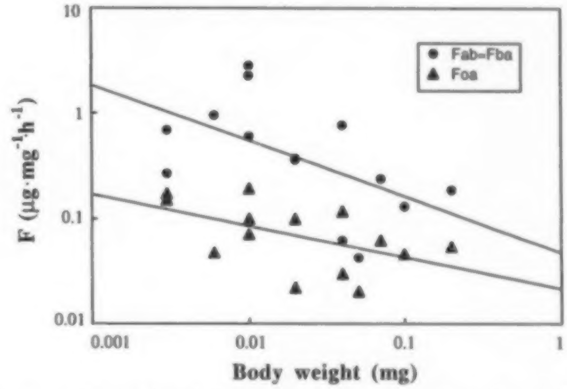

FIG. 6. Allometric relations describing the size dependence of intercompartmental exchange and exit flux rates.

General Discussion

Compartmental Modelling of P Fluxes

Our results demonstrate that P fluxes in cladocerans could be modelled with a two-compartment system (Fig. 6). This is consistent with Lampert and Gabriel (1984), who also found that the ^{14}C dynamics in *Daphnia* followed a two-compartment model. However, we further found that for some cladocerans, a model of more than two pools could better describe the tracer dynamics. This finding may account partially for the large variance in most estimated model parameters. As Shipley and Clark (1972) pointed out, combining three-, four-, or more compartments into a working model with only two compartments may introduce errors.

We demonstrated that in all the cladocerans investigated, the relative pool size of rapidly exchanging pools was much smaller than the slowly exchanging pools, agreeing with pre-

TABLE 4. Comparison of size-specific P release rates of limnetic zooplankton measured by different techniques. W = body dry weight (μg), T = temperature (°C), RR = release rate (μg P·mg^{-1}·h^{-1}), M = method of measurement, na = data not available.

Species	W	T	RR	M	Investigator
D. magna	250	20–22	0.032	Radiotracer	Rigler 1961
D. pulex	21	10–25	0.927	Radiotracer	Whittaker 1961
Cladocera	0.9	5–20	0.085–0.190	Chemical	Barlow and Bishop 1965
D. rosea	13.4	20–22	0.08	Radiotracer	Peters and Lean 1973
D. galeata	1–10	20	0.30–1.10	Radiotracer	Peters 1975
Zooplankton	4–12	15	0.04–0.08	Chemical	LaRow 1971
Daphnia spp.	na	10–20	0.16–0.39	Chemical	LaRow et al. 1975
D. pulex	20	20	0.15–0.21	Chemical	Lehman 1980
Zooplankton	10–70	20	0.32–0.80	Modelling	Bartell 1981
Daphnia spp.	10–48	15–16	0.05–1.5	Chemical	Olsen and Østgaard 1985
Zooplankton	1–5	18–20	0.17	Chemical	den Oude and Gulati 1988
D. longispina	2–>55	na	0.23–1.06	Radiotracer	James and Salonen 1991
			0.14–0.7	Modelling	
Cladocera	3–200	20	0.02–0.19	Radiotracer	Present study

TABLE 5. Results of a simulation to show the effects of incubation time and number of compartments on the cladoceran P excretion rates (μg·mg^{-1}·h^{-1}).

Number of compartments	Incubation time (h)	Body size (mg)			
		0.001	0.01	0.1	1
2	1	1.31	1.64	1.33	0.77
	5	0.47	0.46	0.62	0.59
	10	0.36	0.28	0.35	0.43
	30	0.29	0.16	0.14	0.19
	50	0.27	0.13	0.10	0.12
	100	0.26	0.11	0.07	0.07
1	1	5.67	3.40	1.70	0.83
	5	2.28	2.42	1.63	0.83
	10	1.37	1.64	1.45	0.82
	30	0.68	0.73	0.88	0.73
	50	0.52	0.50	0.62	0.62
	100	0.51	0.49	0.58	0.60

vious results for zooplankton labelled with ^{32}P (Conover 1961; Peters and Rigler 1973) and ^{14}C (Brandl and Fernando 1975; Lampert 1975; Lampert and Gabriel 1984).

There are strong allometries in P release by cladocerans. Smaller species have higher rates per unit body size than large ones. The slope of the regression describing relations between body size and release rates (-0.30 ± 0.11) did not significantly differ from the theoretical expectations of -0.25, which suggests that the allometry of P release in cladocerans is similar to those for other metabolic activities. Our exponent is somewhat higher than that of Peters and Rigler (1973) for *Daphnia* (-0.38), but lower than that recorded by Ejsmont-Karabin (1984) for Cladocera (-0.23) and that for freshwater zooplankton (-0.16) reported by Gutel'makher (1977). These disagreements with the literature values may be due to the experimental protocols that involved different food P levels, zooplankton species, and number of compartments analyzed.

The two-compartment models can only provide an approximate fit to the complex metabolic and structural processes that underlie tracer kinetics. Thus, one could always fit more compartments, if the data are sufficiently numerous. However, given the quality of available data, models involving more than two or three compartments are rarely justified. The surprisingly steep allometric slopes describing intercompartmental exchanges may reflect an adustment in fitting multicompartmental processes to a two-compartment model. In other words, the anomalously steep exponents for the exchange rates between the compartments may reflect the net effect of second-, or higher order exchanges involving several interacting compartments.

Our model provides a new quantitative insight into P release in cladocerans. A crude comparison shows that the excretion rates of P we measured fall in the lower range of literature values (Table 4). Our rates are very close to those of Rigler (1961), Barlow and Bishop (1965), LaRow (1971), Peters and Lean (1973), and Olsen and Østgaard (1985). Although our rates refer to total P, and not just to biologically available PO_4, Peters and Lean (1973) showed that most of the P excreted by *Daphnia* was PO_4 (90%) and even soluble organic forms may be available. Our relatively low P excretion rates probably reflect the use of P-starved yeast as food. Other possible sources of underestimation inherent to the technique employed could be responsible: P sinks via growth, reproduction, and ecdysis (Peters and Rigler 1973) were not measured. Other comparisons are difficult to make because literature estimates of P release rate are highly variable (Peters 1987b) and often reflect methodological and environmental influences. All of the following affect zooplankton excretion rates to some extent: reuptake of excreta by animals (Ganf and Blazka 1974; Takahashi and Ikeda 1975; Blazka et al. 1982) and by epizootics living on the zooplankton (Rigler 1961; Peters and Lean 1973), starvation (Takahashi and Ikeda 1975), injury (Mullin et al. 1975; Ikeda et al. 1982), reproductive stage (Scavia and McFarland 1982), size of the experimental animals (Johannes 1964; Ikeda et al. 1982; Peters 1983; Ejsmont-Karabin 1984), incomplete labelling of animals (Peters and Rigler 1973; Peters 1975), and quantity and quality of the diet (Scavia and Gardner 1982; Lehman and Naumoski 1985; Olsen and Østgaard 1985; Sterner 1990). Further studies are required to examine the contributions of these potential sources of error to the variability of ^{32}P release rates.

Validity of the Feeding and Flux Allometries

Few workers have attempted to estimate cladoceran P ingestion rates by a radiotracer technique as we did, so its validity should be examined. Because our results show that the estimated ingestion rates are sufficient to sustain excretion, an indirect test is possible by comparing our ingestion rates with others in the literature. Reported ingestion rates (reviewed in Chow-Fraser and Sprules 1992) are generally similar to those we measured, which also fall within the range predicted by the empirical model of Peters and Downing (1984) for cladocerans. Because their model was based on a large number of literature values, this consistency supports our data for both ingestion and excretion. We also showed that ingestion in cladocerans is a size-dependent process, with the specific rates decreasing with body size at a rate constant close to -0.25, again in good agreement with general trends (Peters 1983, 1984). Consequently, our equation provides information about P flux that seems both physiologically meaningful and quantitatively reliable.

Our estimates of P assimilation efficiency seem typical for zooplankton if somewhat high. Lampert (1987) indicated that the assimilation efficiencies of *Daphnia* species varied nearly 10-fold (10.5–100%) in the literature, depending on the food concentration and quality, temperature, nutritional state, and physiological condition of the animals. Schindler (1971) found similar variation in assimilation efficiencies for *D. longispina* feeding on different foods. Our calculated P assimilation efficiencies are at the high end of the range reported by Rigler (1961) for *D. magna* (40%), Haney (1971) for *D. galeata medotae* and *D. rosea* (60%), Peters and Rigler (1973) for *D. rosea* (0–100%), James and Salonen (1991) for *Daphnia* sp. (52.6–63.3%), and Taylor and Lean (1991) for lake zooplankton (21–63%) but are comparable with those by Marshall and Orr (1955) for *Calanus* spp. (15–99%) and Berner (1962) for *Temora longicornis* (50–98%). Our values may be higher because the yeast was grown in P-limited cultures to increase assimilation of the label; Olsen and Østgaard (1985) have noted that when food P is in low supply, P assimilation is high and P release is low. Our estimates seem more reliable than previous ones because our values fall in the range of these measured for various food items and are less variable. It is clear that compartmental analysis can provide fairly good estimates for assimilation rates for cladocerans.

Our two-compartment model also allows a quantitative assessment of the effects of nonuniform labelling and of compartment numbers on the cladoceran P excretion rates (Table 5). To evaluate the effect of incomplete labelling, the model of Fig. 1 and equations (1) and (2) with their parameters set by the allometric equations (11–14) and (17) were used to estimate the distribution of the tracer in compartments *a* and *b*. After 1, 5, 10, 30, 50, and 100 h of "feeding" on radioactive food, these model animals were no longer given labelled diet to simulate the dynamics of ^{32}P excretion and to estimate P excretion rate. Excretion rate was estimated as the product of pool size *a* and excretion rate constant (k_{oa}). Pool size *a*, the amount of P in compartment *a* at time *t*, was calculated as $0.0126W{\cdot}Q_a/(Q_a + Q_b)$, where Q_a and Q_b are the amount of tracer in compartments *a* and *b*, *W* is animal dry weight in (milligrams), and 0.0126 is the proportion of P in cladocerans. The results (Table 5) clearly indicate that the further the animals depart from equilibrium of tracer and tracee atoms between ^{31}P and ^{32}P (the shorter the incubation time), the larger the overestimation of excretion rates (5–19 times between 1 and 100 h of radioactive labelling). It is also apparent that the larger the animal, the longer time is required for isotopic equilibrium with the P source. We also estimated the one-compartment P excretion rates. We fitted a one-compartment model to the excretion data derived from the model with two compartments and extrapolated the regression line to $t = 0$ at which point the intercept represents the loss rate of P from the single compartment (Peters and Rigler 1973). As shown in Table 5, treating a two-compartment system as though it consisted only of one compartment may result in an overestimation up to 1 order of magnitude, depending on the animal size and labelling time.

Acknowledgements

We thank Drs. W.D. Taylor, J. Kalff, N. Price, and J. Rasmussen for their helpful comments and suggestions to improve the manuscript. The Natural Sciences and Engineering Research Council of Canada (NSERC), Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR), and the Graduate Faculty of McGill University provided financial support.

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Importance of Wetlands as Sources of Methyl Mercury to Boreal Forest Ecosystems[1,2]

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St. Louis, V.L., J.W.M. Rudd, C.A. Kelly, K.G. Beaty, N.S. Bloom, and R.J. Flett. 1994. Importance of wetlands as sources of methyl mercury to boreal forest ecosystems. Can. J. Fish. Aquat. Sci. 51: 1065–1076.

Wetlands were found to be important sources of methyl mercury to the boreal forest ecosystem. Yields of methyl mercury were about 26–79 times higher from wetland portions of catchments (1.84–5.55 $mg \cdot ha^{-1} \cdot yr^{-1}$) than from purely upland areas (0.07 $mg \cdot ha^{-1} \cdot yr^{-1}$). Mass-balance estimates using methyl mercury inputs in wet deposition and outputs in runoff water indicated that purely upland catchments and lakes were sites of methyl mercury retention or demethylation, while catchments with wetland areas were sites of net methyl mercury production. These observations may explain the high concentrations of mercury in fish taken from lakes that are high in colour because they receive water from wetlands. There was no relationship between the concentration of total mercury and the concentration of methyl mercury in runoff water. Total mercury yields were low from a wetland-dominated catchment, higher from a combination upland/riparian wetland catchment, and highest from a purely upland catchment. The opposite was true for methyl mercury yields from these same catchments. This indicates that environmental factors other than total mercury concentration are controlling the production and loss of methyl mercury from catchments.

On a constaté que les milieux humides sont d'importantes sources de méthyl-mercure dans l'écosystème forestier boréal et que la production de ce composé est de 26 à 79 fois supérieure dans les secteurs humides de bassins hydrologiques (1,84–5,55 $mg \cdot h^{-1} \cdot an^{-1}$) à ce qu'elle est dans les hautes terres (0,07 $mg \cdot ha^{-1} \cdot an^{-1}$). Les estimations des bilans de masse qui tiennent compte des apports en méthyl-mercure par dépôt humide et des pertes dans l'eau de ruissellement indiquent que les bassins hydrologiques constitués uniquement de hautes terres et que les lacs sont des sites de rétention du méthyl-mercure ou d'une déméthylation tandis que les bassins hydrologiques qui comportent des milieux humides sont des sites de production nette de méthyl-mercure. Il se peut qu'on puisse expliquer ainsi la forte concentration en mercure du poisson provenant de lacs aux eaux fortement colorées puisque ces lacs reçoivent des eaux provenant de milieux humides. Il n'y a pas de rapport entre la concentration en mercure total et la concentration en méthyl-mercure dans l'eau de ruissellement. On a observé que la production de mercure total dans un bassin hydrologique dominé par les milieux humides est faible, celle d'un bassin hydrologique constitué de hautes terres et de milieux humides riverains est supérieure, et celle provenant d'un bassin hydrologique constitué uniquement de hautes terres est la plus élevée. Cette relation est inversée dans le cas du méthyl-mercure. Cela indique que des facteurs environnementaux autres que la concentration en mercure total agissent sur la production et la perte de méthyl-mercure dans les bassins hydrologiques.

Received April 27, 1993
Accepted December 9, 1993
(JB904)

Reçu le 27 avril 1993
Accepté le 9 décembre 1993

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[1] Contribution No. 1 of the Experimental Lakes Area Reservoir Project (ELARP).

[2] This is one of a series done in honour of the 25th anniversary of the Experimental Lakes Area.

Virtually all mercury in fish flesh is methyl mercury (Bloom 1992) that has been accumulated from the water or through the food web. Possible sources of this methyl mercury in food and water are production by bacteria within the lake (e.g., Winfrey and Rudd 1990) and inputs from precipitation and watersheds (Bloom and Watras 1989; Lee and Hultberg 1990; Lee and Iverfeldt 1991). The relative importance of each of these sources to fish mercury concentrations has not been determined for drainage lakes and probably varies widely from case to case.

In southwestern Sweden, where fish from many drainage lakes have unacceptably high mercury concentrations, Hultberg and Iverfeldt (1992) recently reported that inputs of methyl mercury from atmospheric deposition are sufficient to account for the high fish mercury concentrations. Atmospheric deposition of methyl mercury is unlikely to be as important in remote near-pristine regions of the Canadian boreal forest. In the Canadian boreal forest, fish from many lakes have commercially acceptable mercury concentrations (i.e., $<0.5\ \mu g \cdot g^{-1}$), while fish in neighbouring lakes that receive the same precipitation have concentrations well in excess of $0.5\ \mu g \cdot g^{-1}$ (e.g., Bodaly et al. 1993).

These interlake differences in fish mercury concentrations could result from differences in in-lake methyl mercury production, differences in bioavailability of methylated mercury, and/or differences in methyl mercury inputs from dissimilar types of watersheds surrounding lakes. Type of watershed (e.g., wetland or upland) affects total mercury inputs to lakes (Mierle and Ingram 1991), but this has not been examined for methyl mercury.

We recently began measuring export of methyl and total mercury from a variety of boreal forest catchments at the Experimental Lakes Area (ELA) in northwestern Ontario. We have also measured wet precipitation inputs of methyl mercury, showing that in the relatively pristine ELA region, these inputs were low compared with more polluted areas such as southwestern Sweden. Export of methyl mercury from ELA catchments that contained wetlands was much higher than precipitation inputs and higher from either forested upland catchments or a catchment that contained six lakes. Together, these data indicate that wetlands are important sites of methyl mercury production in near-pristine boreal ecosystems.

Methods

Catchment Types

In 1991, we measured the concentration and yield of total and methyl mercury in water flowing from four types of boreal forest catchments: (1) an upland terrain catchment (U), (2) a combination of upland terrain with riparian wetland (U/W), (3) a catchment dominated by a headwater wetland (W), and (4) a catchment containing three stratified and three unstratified lakes (L) plus upland and wetland areas (Fig. 1). The sites were chosen to represent major catchment types found in the boreal forest and are characterized below.

(1) The U catchment was 5.73 ha with southern exposure and a fairly uniform slope that culminated at a recording weir on an inflow stream 133 m upstream from Lake 114 (Fig. 1). Ground cover consisted of thin glacial till covered with moss and lichen with exposed areas of granodiorite bedrock. The watershed was logged in 1976 and scarified in the early summer of 1979 (Beaty and Lyng 1989), resulting in a young forest dominated by dense stands of young jack pine (*Pinus banksiana* Lamb.) and paper birch (*Betula papyrifera* Marsh.), with interspersed black spruce (*Picea mariana* (Mill.) BSP). This catchment had no low-lying areas or associated wetlands.

(2) There were two U/W catchments, each of which contained a well-developed stream that drained riparian wetlands (wetlands along streams which are occasionally flooded) fed by upland terrain. U/W 1 was a 170.3-ha catchment that drained into the east bay of Lake 239, and U/W 2 was a smaller 55.3-ha catchment that drained into the Lake 979 pond (Fig. 1). Both U/W catchments were burned in 1974 and 1980 by naturally occurring forest fires (Bayley et al. 1992). As a result, the forest regeneration in both catchments was similar and was dominated by fire succession plants, mainly jack pine and paper birch, with some black spruce. The uplands drained into riparian wetlands dominated by paper birch, alder (*Alnus* spp.), and black spruce, with mosses including *Sphagnum* spp. as ground cover.

(3) The W catchment contained 36 ha of predominately upland that drained into a 3.4-ha headwater wetland with a central pond (0.8 ha; Fig. 1). The outflow from the catchment was hydrologically monitored at a weir installed at the edge of the wetland 185 m downstream of the pond (Fig. 1). A portion of W was logged about 1973–74. This area contained young jack pine, black spruce, balsam fir (*Abies balsamea* (L.) Mill.), paper birch, and maple (*Acer* spp.), with some *Alnus* spp. understory. The unlogged area was a mature jack pine, black spruce, and paper birch forest. The major wetland plants were *Sphagnum* spp., with an overstory of black spruce, larch (*Larix laricina* (Du Roi) K. Koch), Labrador tea (*Ledum groenlandicum* Oedes), and leatherleaf (*Chamedaphne calyculata* (L.) Moench). *Carex* spp. and *Sphagnum* spp. dominated the vegetation along the stream edge.

(4) The L catchment (Lake 240 watershed of which U/W 1 was a part) was 723 ha and contained three stratified and three unstratified lakes (Fig. 1). Several wetlands adjoined lakes and connecting streams. Portions of the watershed were burned by forest fire in 1974 whereas the remainder of the watershed was burned in 1980. As a result, the majority of the watershed was dominated by dense stands of young jack pine and paper birch, with some black spruce, as described for U/W 1 and U/W 2.

General Catchment Hydrology

Water generally flowed all year from lakes and wetland ponds (L and W). Snowfall and freeze-up usually began in early November and lakes and ponds remained continuously ice-covered until the end of April (approximately 165 d). Snow that accumulated on the ice surface displaced water out the outflows, resulting in flow during the winter period originating from lake or pond water rather than from precipitation. In the terrestrial basins (U, U/W 1, and U/W 2), stream flows were episodic depending on antecedent moisture conditions and sustained by rainfall events from May to October. In November, terrestrial flows diminished and remained low or zero throughout the winter. Snow accumulated in the terrestrial basins until it melted in April to produce spring runoff.

Flow volumes were estimated either from monitored flow records from weirs, manual measurements, or extrapolated record from other nearby stations (flow between basins

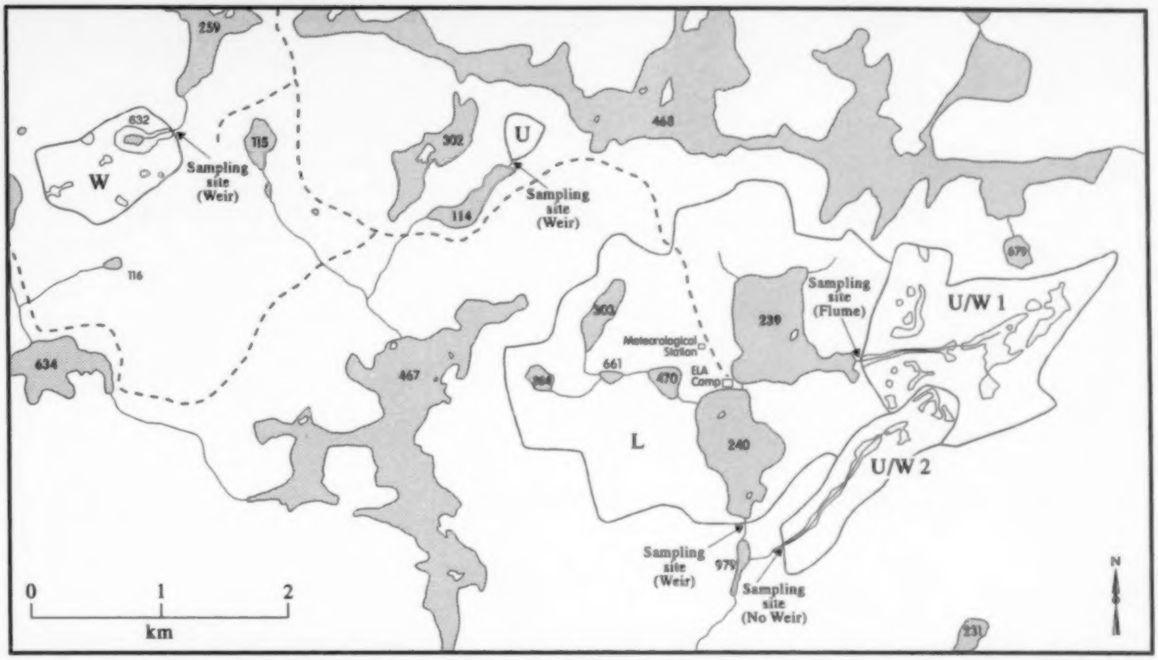

FIG. 1. Location of the catchments and sampling sites at the Experimental Lakes Area (ELA), northwestern Ontario. Dark shaded areas are lakes. Light shaded areas within each catchment are wetland areas (*Sphagnum* spp. carpets and valley marshes). Wetland areas within the majority of the L catchment are not shown because in-lake processes dictate the characteristic of water flowing from this catchment (see Table 5). U/W 1 is part of the L catchment. The broken line is a logging road to the ELA camp.

through fractures in the granitic bedrock of ELA basins is minimal (K.G. Beaty and M. Stephenson, personal communication)). At the U catchment, flows were measured continuously through a 90° v-notch weir with a stage recorder from the beginning of spring runoff until freeze-up. Flow volume at the U/W 1 catchment was similarly monitored through a shallow v-notch flume. Due to the lack of a suitable monitoring site in the U/W 2 basin, flow estimates were determined on a runoff per unit area extrapolation of the nearby U/W 1 catchment flow record. The two catchments were very similar with respect to geology and basin physiography. Hydrological monitoring of the W site began with the construction of a 90° v-notch recording weir in June 1991. Flow volume estimates for the earlier part of 1991 for the W site were based on a runoff per unit area extrapolation of the nearby Lake 373 outflow record. The outflow of site L was monitored continuously with a 120° v-notch weir equipped with a stage recorder and data logger. At all sites, winter visits were made routinely each month to check for the presence of flow and to measure if necessary. In the absence of monitored record, flow estimates were made between these observations by interpolation.

Sampling Methods and Analytical Methodologies

Total and methyl mercury concentrations were sampled weekly during high spring flow, biweekly during the low-flow summer period, and monthly at sites that flowed during winter. Duplicate samples were taken at each site in either 125- or 250-mL Teflon bottles. The bottles were first washed in hot HNO_3, filled with a 1% HCl solution, and then stored in two new Ziploc bags. Bottles were transported to the field in clean coolers that were placed inside two plastic bags. At the sampling site, the "clean hands, dirty hands" protocol was used. This protocol requires two people to vigorously wash their gloved hands in sample site water; however, only one person touches the inside bag and the sample bottle itself whereas the other person handles the outside bag. The 1% HCl solution in the bottle was drained, and the bottle was then rinsed three times with sample site water before filling and being replaced into the bags. Exactly 125 or 250 μL of concentrated trace metal grade HCl was added to 125- or 250-mL samples, respectively, within 2 h of sample collection, again using the clean hands, dirty hands protocol. Flett Research Ltd., Winnipeg, Man., analyzed unfiltered samples for total mercury using the technique of Bloom and Crecelius (1983). The detection limit of this method is 0.2–0.3 ng·L^{-1} at a blank level of 0.3–0.4 ng·L^{-1}. Unfiltered methyl mercury samples were analyzed by Brooks Rand, Ltd., Seattle, Wash., using Bloom's (1989) procedure. The detection limit of this method is 0.01–0.02 ng·L^{-1} at a blank level of 0.05–0.1 ng·L^{-1}. Water samples collected coincidentally with the mercury samples were analyzed using Stainton et al. (1977) for nitrate nitrogen (NO_3^--N), nitrite nitrogen (NO_2^--N), ammonium nitrogen (NH_4^+-N), total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), colour (measured by a colorimetric method designed to emulate Hazen Units; see Mierle and Ingram 1991), sulfate (SO_4^{2-}), chloride, sodium, potassium, magnesium, calcium, iron, manganese, specific conductance, alkalinity, and pH.

Wet Deposition

In the latter part of 1992, we analyzed for concentrations of total and methyl mercury in wet deposition to determine

TABLE 1. Concentrations of chemical substances in water flowing from the different catchments used in this study. Values are means (±SE) of all (*N*) sampling events in 1991. Numbers in parentheses are samples sizes that deviate from samples sizes given in the *N* row.

	U	U/W 1	U/W 2	W	L
N	8	15	9	19	26
NO_3^--N ($\mu g \cdot L^{-1}$)	1.00 ± 0.27	187.47 ± 63.48	54.00 ± 15.77	9.79 ± 2.83	11.63 ± 3.34
NO_2^--N ($\mu g \cdot L^{-1}$)	0.88 ± 0.13	1.87 ± 0.39	1.78 ± 0.32	1.53 ± 0.26	0.00 ± 0.00
NH_4^+-N ($\mu g \cdot L^{-1}$)	9.75 ± 1.53	37.93 ± 7.49	21.56 ± 2.51	29.74 ± 4.49	20.75 ± 3.70
TDN ($\mu g \cdot L^{-1}$)	281.25 ± 13.02	836.67 ± 86.77	574.44 ± 44.82	382.11 ± 17.23	266.25 ± 5.76
TDP ($\mu g \cdot L^{-1}$)	6.00 ± 0.50	11.20 ± 0.90	7.44 ± 0.56	4.32 ± 0.42	2.69 ± 0.37
DIC ($\mu mol \cdot L^{-1}$)	74.25 ± 4.93	262.18 ± 16.87	277.00 ± 33.09	365.67 ± 40.93	171.08 ± 5.43
DOC ($\mu mol \cdot L^{-1}$)	1180.00 ± 53.59	2098.67 ± 92.11	1621.11 ± 134.60	1399.47 ± 71.06	531.88 ± 13.11
Colour (Hazen Units)	0.295 ± 0.000 (1)	0.688 ± 0.052 (8)	0.670 ± 0.078 (8)	0.572 ± 0.036 (16)	0.042 ± 0.002 (14)
SO_4^{2-} ($mg \cdot L^{-1}$)	4.22 ± 0.07	7.53 ± 0.36	6.47 ± 0.53	2.29 ± 0.19	4.41 ± 0.14
Cl^- ($mg \cdot L^{-1}$)	0.30 ± 0.03	0.27 ± 0.04 (14)	0.26 ± 0.05	0.17 ± 0.02 (18)	0.40 ± 0.01
Na^+ ($mg \cdot L^{-1}$)	0.63 ± 0.01	1.60 ± 0.05	1.31 ± 0.02	0.94 ± 0.04	1.18 ± 0.03
K^+ ($mg \cdot L^{-1}$)	0.37 ± 0.02	0.44 ± 0.07	0.17 ± 0.03	0.22 ± 0.02	0.71 ± 0.02
Mg^{2+} ($mg \cdot L^{-1}$)	0.48 ± 0.01	1.29 ± 0.05	0.95 ± 0.06	0.49 ± 0.01	0.91 ± 0.02
Ca^{2+} ($mg \cdot L^{-1}$)	1.44 ± 0.05	4.04 ± 0.15	2.77 ± 0.16	1.38 ± 0.04	2.98 ± 0.08
Fe^{2+} ($mg \cdot L^{-1}$)	0.29 ± 0.02	0.37 ± 0.03	0.27 ± 0.04	0.20 ± 0.02	0.02 ± 0.00
Mn^{2+} ($mg \cdot L^{-1}$)	0.01 ± 0.00	0.02 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00
Conductivity ($\mu S \cdot cm^{-1}$)	22.50 ± 0.82	40.40 ± 1.20	32.33 ± 1.14	19.74 ± 0.57	31.38 ± 0.71
Alkalinity ($\mu Eq \cdot L^{-1}$)	−8.25 ± 1.22	73.60 ± 7.76	27.67 ± 2.97	13.58 ± 4.67	154.06 ± 3.83
pH	4.82 ± 0.03	5.55 ± 0.11	5.26 ± 0.05	5.06 ± 0.06	7.19 ± 0.05

the amount of mercury in rainwater entering the watersheds. Concentrations of mercury in wet deposition were not measured in 1991. Wet deposition samples were collected at the ELA meteorological station (Fig. 1) in wide-mouthed Teflon containers (11.5-cm diameter, 5-cm height) that were prepared as described above for the catchment sample bottles. At the beginning of a precipitation event, the 1% HCl solution in four containers was drained using the clean hands, dirty hands protocol, and the containers were placed on four acid-washed Plexiglas trays secured to wooden posts 1.5 m above the ground. Posts were situated in a square approximately 0.6 m apart. Following the end of a precipitation event, samples in the collection containers were transferred to 125-mL Teflon sample bottles, again using the above clean protocol. Samples used for total mercury analyses were acidified with concentrated trace metal grade HCl equal to 1% of the sample volume, while samples used for methyl mercury analyses were immediately frozen.

Presentation of Total and Methyl Mercury Data

Total and methyl mercury data from the catchments are presented both as concentrations and as yields per unit area. It is important to be able to compare mercury concentrations coming from different types of catchments because mercury concentration is one factor that determines mercury bioaccumulation (e.g., Meili 1991a). Yields are important when mass-balance inputs of total and methyl mercury to lakes are being determined. Yields (Y_{Hg}, milligrams) of total and methyl mercury were calculated from each catchment between two sample periods using the equation

$$(1) \quad Y_{Hg} = (([Hg_{t1}] + [Hg_{t2}])/2) \times V$$

where $[Hg_{t1}]$ and $[Hg_{t2}]$ are mean concentrations of either total or methyl mercury in water at two consecutive sampling times and V is the total volume of water that flowed from the catchment between those times (see earlier section on catchment hydrology). Annual yields per unit area (milligrams per hectare per year) of both total and methyl mercury were calculated by summing yields for each sample period for 1991 and dividing by the watershed area.

Concentrations of mercury in water were measured weekly or biweekly at all sites except U, which was dry for most of the summer. Mercury concentrations at U were measured when flow resumed in mid-September. Mercury concentrations in spring at the U catchment were not measured. However, they were estimated as being 6.78 and 0.037 $ng \cdot L^{-1}$ for total and methyl mercury, respectively. These estimated concentrations were the average spring concentrations measured at U in 1992. (Note: we have now followed total and methyl mercury in water flowing from the U catchment for two complete years (fall 1991 to fall 1993, unpublished data). These long-term measurements are consistent with the data presented here.)

Wet deposition loadings (milligrams per hectare) of total and methyl mercury in 1991 were estimated by multiplying the average concentration of mercury in rain and snow from the 1992 measurements by the total rainfall and snowfall water equivalent for 1991 (795.6 mm; K.G. Beaty, unpublished data).

Statistical Analyses

We tested for differences between each catchment in concentrations and yields of total and methyl mercury and percent methyl mercury using t-tests, with P-values calculated using randomization tests (1000 iterations; Edgington 1987). A randomized t-test determines whether t_{obs} is greater than expected by chance. However, because of the large number of t-tests performed (10 paired comparisons for each of total mercury and methyl mercury (concentrations and yields) and percent methyl mercury), P-values were adjusted to an overall $\alpha = 0.05$ level using the sequential Bonferroni method described by Rice (1989). Values used were the concentrations of total and methyl mercury measured at the time of sampling, the percent methyl mercury calculated using concentrations at each of these sampling times, and the yields calculated using equation (1) corrected for catchment area (hectares) and the number of days water flowed between sampling times.

We then asked whether concentrations of either total or methyl mercury were related to water flow. Values used were the total or methyl mercury concentrations at a given sampling time versus the water flow (cubic metres per second) at that time. We tested each of the five catchments separately.

We also asked whether total mercury concentrations were good predictors of methyl mercury concentrations. Here, we compared the concentration of total mercury with the concentration of methyl mercury measured at a given sampling time. First, we tested the data collected throughout the year from each of the five catchments separately. Second, we combined data from all five catchments to see if there was an overall relationship.

We used a Pearson's product moment correlation coefficient (SAS Institute, Inc. 1988) for the correlation analyses. Again, P-values were calculated using randomization tests (1000 iterations). A randomized correlation test determines whether r_{obs} is greater than expected by chance (Jackson and Somers 1991).

Results

Water Chemistry

In general, water flowing from all catchments was dilute (Table 1), as is typical of boreal forest watersheds (Armstrong and Schindler 1971). Concentrations of major cations, anions, and nutrients were, on average, extremely low (Table 1). DOC concentrations were, on average, highest at the U/W 1 catchment, slightly lower and similar amongst the U, U/W 2, and W catchments, and lowest from the L catchment (Table 1). Colour of water flowing from U/W 1, U/W 2, and W was high, intermediate from the U catchment, and lowest from the L catchment. Water flowing from the U, U/W 1, U/W 2, W, and L catchments had average pH's of 4.8, 5.2, 5.6, 5.1, and 7.2, respectively (Table 1), and alkalinity followed a similar pattern (Table 1).

Concentrations of Mercury in Wet Deposition

Rain samples were collected on 7 and 23 August and 7 September 1992, and snow samples were collected on 19 October and 10 November 1992. Concentrations of total mercury in rain and snow were quite low, averaging 3.81 $ng{\cdot}L^{-1}$ (Table 2). Concentrations of methyl mercury in rain and in a single snow sample for 10 November were also low, averaging 0.019 $ng{\cdot}L^{-1}$ (Table 2). Mercury concentrations in rain and snow samples collected the following year (1993; unpublished data) were also low and similar to the 1992 samples reported here.

TABLE 2. Concentrations and yields of total and methyl mercury, and % methyl mercury, in water flowing from the different catchments used in this study. Values for concentrations and % methyl mercury are means (±SE) of all (N) sampling events. Values for yields are means (±SE) of yields calculated using equation (1) corrected for catchment area (ha) and the number of days water flowed between sampling times. N is greater for yields than for concentrations because more than one yield may have been calculated using the same concentrations if water flow stopped and started between sampling times.

	Wet deposition	U	U/W 1	U/W 2	W	L
Concentration total mercury ($ng{\cdot}L^{-1}$)	3.81 ± 0.85 (5)	13.11 ± 0.67 (9)	11.77 ± 0.73 (15)	11.40 ± 0.87 (9)	5.02 ± 0.36 (19)	1.69 ± 0.27 (16)
Yield total mercury ($mg{\cdot}ha^{-1}{\cdot}d^{-1}$)	—	0.265 ± 0.106 (8)	0.152 ± 0.036 (18)	0.139 ± 0.033 (16)	0.048 ± 0.014 (21)	0.012 ± 0.003 (18)
Concentration methyl mercury ($ng{\cdot}L^{-1}$)	0.019 ± 0.004 (4)	0.030 ± 0.006 (9)	0.176 ± 0.012 (15)	0.228 ± 0.033 (9)	0.626 ± 0.126 (19)	0.040 ± 0.003 (16)
Yield methyl mercury ($mg{\cdot}ha^{-1}{\cdot}d^{-1}$)	—	0.0009 ± 0.0005 (8)	0.0018 ± 0.0004 (18)	0.0024 ± 0.0005 (16)	0.0036 ± 0.0007 (21)	0.0003 ± 0.00004 (18)
% methyl mercury	0.63 ± 0.18 (4)	0.23 ± 0.06 (9)	1.58 ± 0.16 (15)	2.04 ± 0.29 (9)	13.31 ± 2.42 (19)	4.37 ± 1.19 (16)

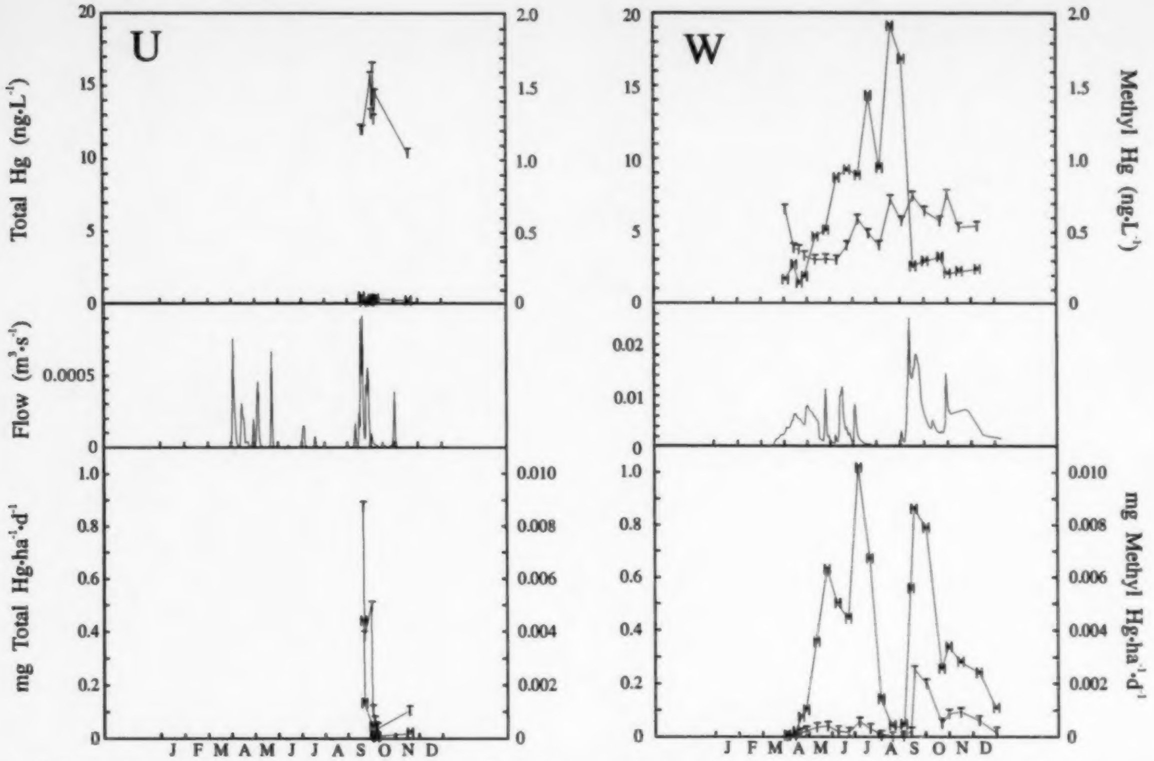

FIG. 2. Seasonal patterns of water flow (middle portion of graphs), concentrations of methyl mercury and total mercury in water (upper portion of graphs), and seasonal estimates of total and methyl mercury yields (lower portion of graphs) at the U and W catchments. T = total mercury; M = methyl mercury.

TABLE 3. Results of correlation analyses (see Methods) of concentrations of total and methyl mercury (ng·L^{-1}) with flow rate (m^3·s^{-1}) at time of sample collection for each of the catchments.

		Total mercury		Methyl mercury	
Catchment	*N*	*r*	*P*	*r*	*P*
U	9	−0.369	0.144	0.636	0.101
U/W 1	15	0.288	0.145	−0.051	0.419
U/W 2	9	−0.151	0.338	0.585	0.076
W	19	0.261	0.148	−0.502	0.005
L	16	0.132	0.310	−0.158	0.298

Concentrations of Mercury in Water Flowing from the Catchments

There was no significant correlation between concentrations of total mercury and flow rates at each of the catchments (Table 3).

Only at the W catchment was there a significant negative correlation between concentrations of methyl mercury and flow rates (Table 3). This result is consistent with dilution of methyl mercury produced within this catchment during periods of high flow.

Concentrations of total mercury in water were generally higher in the fall than in the spring and early summer (Fig. 2–4). For example, water flowing from the U/W catchments (Fig. 3) and L catchment (Fig. 4) increased at the end of a dry period (no flow) which lasted from July to mid-September. The increase in total mercury concentrations in the fall was possibly due to flushing of mercury accumulated as dry deposition during the dry period.

The presence of wetlands or lakes in catchments reduced total mercury concentrations in outflow water. Average concentrations of total mercury were highest in water flowing from the U catchment (13.1 ng·L^{-1}; Tables 2 and 4; Fig. 2) which contains no lakes or wetlands, slightly lower in water flowing from the U/W catchments (11.8 and 11.4 ng·L^{-1}; Tables 2 and 4; Fig. 3) which have mainly riparian wetlands, and significantly lower (Table 4) in water flowing from the W (5.0 ng·L^{-1}; Tables 2 and 4; Fig. 2) and L catchments (1.7 ng·L^{-1}; Tables 2 and 4; Fig. 4) which were dominated by a headwater wetland and lakes, respectively.

Methyl mercury concentrations in water flowing from the catchments had a pattern very different from that observed for total mercury concentrations (Fig. 2–4; Table 2). Average methyl mercury concentrations were always very low in water flowing from the U catchment (0.03 ng·L^{-1}; Tables 2 and 4; Fig. 2), while total mercury concentrations were high. The L catchment, on the other hand, was low in both methyl mercury concentrations (0.04 ng·L^{-1}; Tables 2 and 4; Fig. 4) and total mercury concentrations. Concentrations were significantly higher in water flowing from the U/W catchments (0.176 and 0.228 ng·L^{-1}; Tables 2 and 4; Fig. 3) than in water from the U and L catchments (Table 4). Concentrations

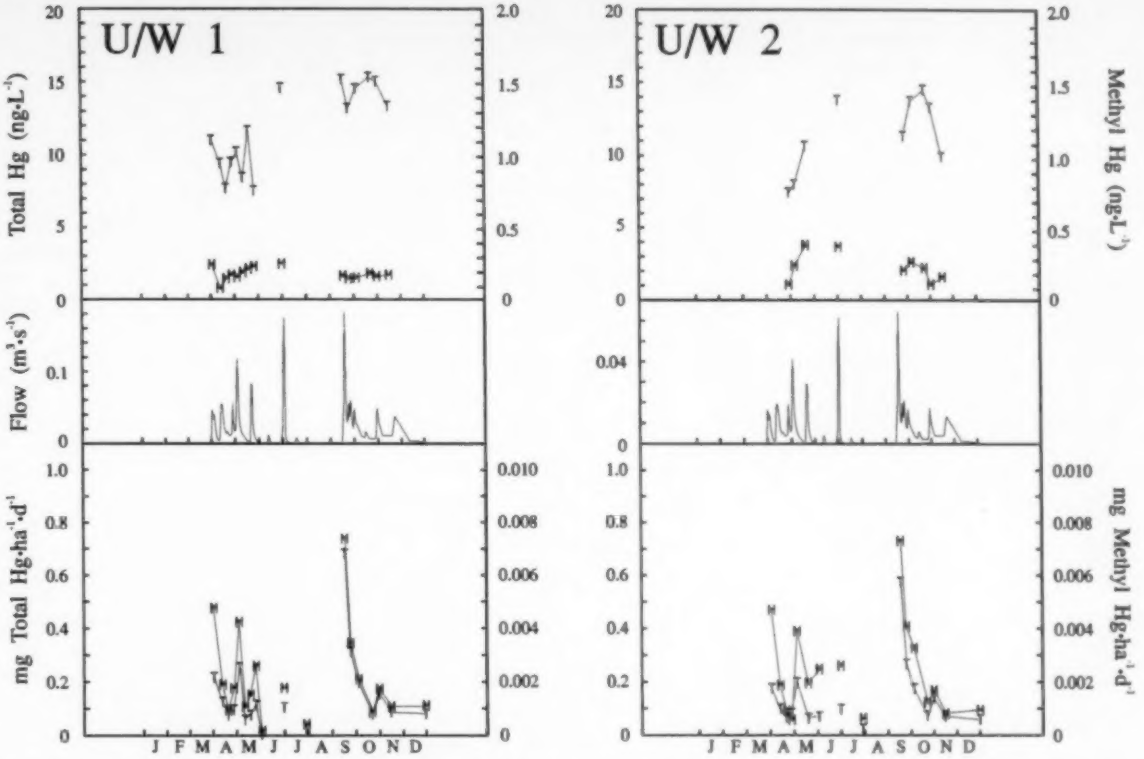

FIG. 3. Seasonal patterns of water flow (middle portion of graphs), concentrations of methyl mercury and total mercury in water (upper portion of graphs), and seasonal estimates of total and methyl mercury yields (lower portion of graphs) at the U/W 1 and U/W 2 catchments. T = total mercury; M = methyl mercury. There was no water flow between unconnected data points.

of methyl mercury in water flowing from the W catchment, which contained the headwater wetland, increased tremendously throughout the summer, peaking at 1.9 ng·L^{-1} just before the end of the summer dry period (Fig. 2). Methyl mercury concentrations then declined sharply as flow increased following a mid-September rain event (Fig. 2). Average concentration of methyl mercury in outflow water from the W catchment was 0.626 ng·L^{-1}, which was about 30-fold greater than the concentration in water flowing from the U catchment that contained no wetland areas (Table 2).

Inputs of Mercury from Wet Deposition

Wet deposition of total mercury to the catchments in 1991 was estimated to be about 30.8 mg·ha^{-1}·yr^{-1} (Table 5). Wet deposition of methyl mercury was estimated to be only about 0.15 mg·ha^{-1}·yr^{-1} (Table 5).

Yields of Mercury from the Catchments

Significantly higher yields of total mercury were associated with catchments dominated by uplands rather than wetlands or lakes (Tables 2, 4, and 5; Fig. 2–4). Yields of total mercury were 20.3 mg·ha^{-1}·yr^{-1} from the upland (U) catchment, slightly lower from the upland catchments with riparian wetlands (U/W catchments; 19.3–22.8 mg·ha^{-1}·yr^{-1}), lower still from the catchment dominated by a headwater wetland (W catchment; 12.2 mg·ha^{-1}·yr^{-1}), and lowest from the lake (L) catchment (3.1 mg·ha^{-1}·yr^{-1}) (Table 5). Yields of total mercury from the individual catchments were highest during periods of high water flow (Fig. 2–4). All yields were lower than wet deposition inputs (Table 5).

High methyl mercury yields were associated with catchments that contained wetlands. Yields of methyl mercury were highest from the W catchment (0.96 mg·ha^{-1}·yr^{-1}), followed by the U/W catchments (0.32–0.35 mg·ha^{-1}·yr^{-1}), and were lowest from the U (0.07 mg·ha^{-1}·yr^{-1}) and L (0.06 mg·ha^{-1}·yr^{-1}) catchments (Tables 2, 4, and 5; Fig. 2–4). Most of the methyl mercury yield occurred during periods of high water flow within the individual catchments (Fig. 2–4). Only the U and L catchments appeared to retain methyl mercury inputs when compared with estimated inputs from wet deposition (Table 5).

To more clearly illustrate that wetlands are important sources of methyl mercury, we separately estimated yields of methyl mercury from the upland and wetland portions of the three catchments that contained wetlands (U/W 1, U/W 2, and W). This was done by assuming that the methyl mercury yields from the purely upland portions of the U/W and W catchments were equal to the areal yield of methyl mercury from the U catchment. We found that in each case the yield per area of the purely wetland portions of the U/W and W catchments was approximately 5.7 times higher than from the catchment as a whole (Table 5). Because the purely upland catchment (U) appeared to retain or demethylate mercury whereas catchments containing wetlands were net methyl mercury producers, the differences in methyl mercury yields

TABLE 4. Results from *t*-tests comparing each catchment with the others for concentrations and yields of total and methyl mercury, and % methyl mercury. Catchments are listed in order from highest mean on the left to lowest mean on the right. Means (±SE) are listed in Table 2. Catchments joined by the same line are not significantly different from each other. Because of the large number of *t*-tests performed (10 paired comparisons for each of total mercury, methyl mercury, and % methyl mercury), *P*-values were adjusted to an overall $\alpha = 0.05$ level using the sequential Bonferroni method (see Methods).

Total mercury concentrations	U	U/W 1	U/W 2	W	L
Total mercury yields	U	U/W 1	U/W 2	W	L
Methyl mercury concentrations	W	U/W 2	U/W 1	L	U
Methyl mercury yields	W	U/W 2	U/W 1	U	L
% methyl mercury	W	L	U/W 2	U/W 1	U

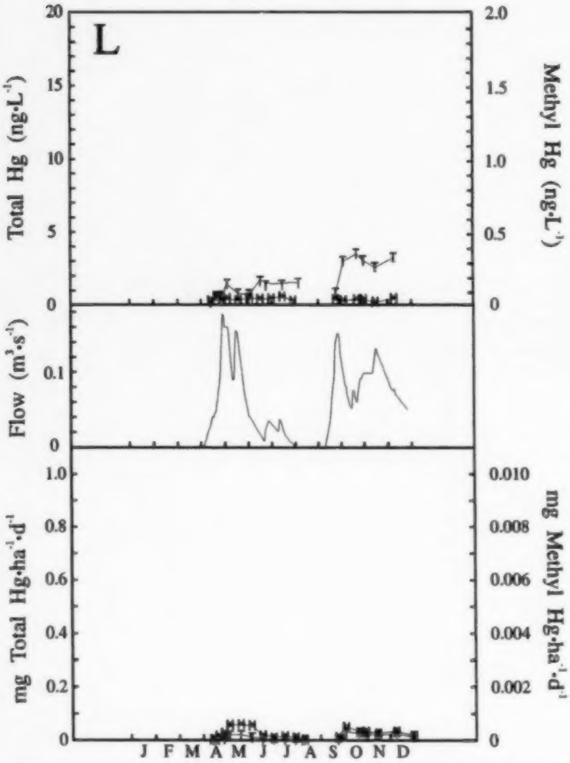

FIG. 4. Seasonal pattern of water flow (middle portion of graph), concentrations of methyl mercury and total mercury in water (upper portion of graph), and seasonal estimates of total and methyl mercury yields (lower portion of graph) at the L catchment. T = total mercury; M = methyl mercury. There was no water flow between unconnected data points.

between purely upland and wetland-containing catchments was very high (about 26-, to 79-fold).

Relationships between Total and Methyl Mercury

Methyl mercury concentrations in water amongst all catchments and sampling periods were not significantly correlated with concentrations of total mercury in the water ($r = -0.105$, $P = 0.212$) (Fig. 5). This lack of correlation also existed when the data were separated according to catchment type (Table 6; Fig. 5). This suggests that rates of methylation were not directly related to the concentration of total mercury available for methylation at any given time.

There were large catchment-to-catchment differences in percent methyl mercury measured using concentrations. The W catchment, which had the highest yield of methyl mercury, also had a significantly higher percent methyl mercury than all other catchments (13.3%; Tables 2 and 4). The U catchment, which yielded very little methyl mercury but had the highest yield of total mercury, had a significantly lower percent methyl mercury than the other catchments (0.23%). In contrast, the L catchment, which had low yields of both methyl mercury and total mercury, had a significantly higher percent methyl mercury than the U catchment (4.37%). The percent methyl mercury at the L catchment was significantly higher than from the U/W 1 catchment (1.58%; Tables 2 and 4) but no different from the U/W 2 catchment (2.04%).

Discussion

This study shows that wetlands are important sources of methyl mercury to boreal ecosystems. We conclude this because yields of methyl mercury from catchments containing wetlands were significantly higher (5- to 14-fold) than from a purely upland catchment (Fig. 2–4; Tables 2 and 4). Further, when we calculated separately methyl mercury yields from the upland and wetland portions of our mixed catchments (U/W 1, U/W 2, and W), the contribution per unit area from the wetland portion was estimated to be 26–79 times greater than from purely upland terrain (Table 5).

While wetlands in general yielded high amounts of methyl mercury, there were differences in methyl mercury yields from one type of wetland to another. The headwater wetland yielded methyl mercury at about three times the rates of the riparian wetlands annually (Table 5). This may have been related to the longer water residence time of the headwater as compared with the riparian wetlands.

Because yields of methyl mercury from the wetlands were much higher than inputs from both precipitation and the upland terrain (Table 5), methyl mercury must have been produced in the wetlands by chemical or microbial processes. Lee and Hultberg (1990) concluded that most of the methyl mercury in upland soils was produced by chemical methyl-

TABLE 5. Estimated annual wet deposition of total and methyl mercury to, and annual yields of total and methyl mercury from, the catchments used in this study.

	Wet deposition[a]	U	U/W 1	U/W 2	W	L
Catchment area (ha)	—	5.7	170.3	55.3	40.2	723.0
% wetland[b]	—	0	14.0	14.4	16.3	0[c]
Upland area (ha)	—	5.7	146.5	47.3	33.7	723.0
Wetland area (ha)	—	0	23.8	8.0	6.5	0
Yield total mercury ($mg \cdot yr^{-1}$)	—	116.35	3886.33	1068.80	492.73	2236.89
Yield methyl mercury ($mg \cdot yr^{-1}$)	—	0.41	54.36	19.36	38.71	43.22
Yield total mercury ($mg \cdot ha^{-1} \cdot yr^{-1}$)	30.8	20.31	22.82	19.33	12.26	3.09
Yield methyl mercury ($mg \cdot ha^{-1} \cdot yr^{-1}$)	0.15	0.07	0.32	0.35	0.96	0.06
% methyl mercury yield[d]	0.49	0.35	1.40	1.81	7.86	1.93
Estimated yield of methyl mercury from wetland area only ($mg \cdot ha^{-1} \cdot yr^{-1}$)[e]	—	—	1.84	2.00	5.55	—

[a] Yields estimated from mercury concentrations averaged from wet deposition events in 1992 (see Table 2).

[b] % wetland areas within each catchment calculated from digitized tracings of aerial maps (1:16000). *Sphagnum* spp. carpets and valley marshes were considered wetland areas.

[c] Although there are wetland areas within the L catchment, in-lake processes dictate the characteristic of water flowing from this catchment. Mean 1969–90 residence time in Lake 240, the last lake in a series of six, is 1.47 yr (K.G. Beaty, unpublished data).

[d] % methyl mercury yields calculated using annual yields of total and methyl mercury (see Table 2 for % methyl mercury calculated using concentrations only).

[e] Value derived by subtracting yield ($mg \cdot yr^{-1}$) of methyl mercury from upland proportion of catchment from total catchment yield ($mg \cdot yr^{-1}$) and dividing remaining methyl mercury yield by area of wetland (ha).

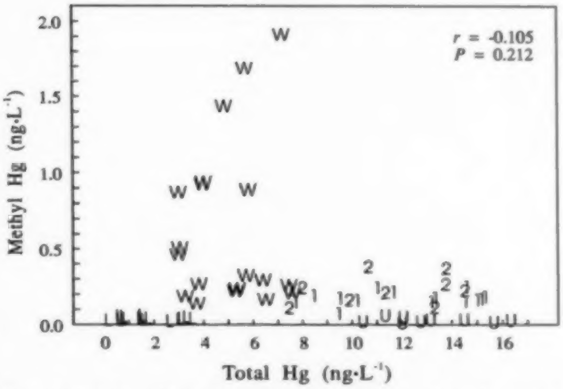

FIG. 5. Relationship between concentrations of total mercury and concentrations of methyl mercury. Symbols for catchments U/W 1 and U/W 2 have been abbreviated to 1 and 2, respectively. See Table 6 for the relationships between concentrations of total mercury and concentrations of methyl mercury within each of the catchments.

TABLE 6. Results of correlation analyses (see Methods) of concentrations of total mercury ($ng \cdot L^{-1}$) with concentrations of methyl mercury ($ng \cdot L^{-1}$) for each of the catchments (also see Fig. 5).

Catchment	*N*	*r*	*P*
U	9	−0.283	0.246
U/W 1	15	0.057	0.426
U/W 2	9	0.296	0.213
W	19	0.085	0.359
L	16	−0.080	0.394

ation by DOC. However, the concentrations of inorganic mercury and DOC used in their experiments were 10^6 and 10 times higher, respectively, than the natural concentrations found in our wetlands (Tables 1 and 2). Therefore, it is more likely that in these wetlands the methylation was microbially mediated, as concluded by Berman and Bartha (1986).

Microbial methylation is controlled by a number of environmental factors, some of which may enhance methylation in wetlands. Total mercury concentration was apparently not important in our study because we saw no relationship between total and methyl mercury concentrations (Table 6; Fig. 5; also note the range of percent methyl mercury amongst catchments in Table 2). However, the availability of inorganic mercury for methylation in our wetlands may be enhanced because of the low pH, as has been found in low-pH lake water (Xun et al. 1987; Miskimmin et al. 1992). Sulfate reducers may be important methylators (Gilmour and Henry 1991). Sulfate reduction is an important microbial activity in the wetland (W) catchment, as shown by the low sulfate concentrations at the outflow (Table 1) and in other wetlands (e.g., Bayley et al. 1987). Methylation has been shown to be positively correlated with temperature (Bodaly et al. 1993; Ramlal et al. 1993), and there did appear to be stimulated rates of methylation at these sites during the summer months when water temperatures were at their highest (Fig. 2 and 3). However, water flowing from the wetlands was generally cold (average sampling time temperatures at the U/W 1, U/W 2, and W catchments were 5.4–8.7°C in 1991). Wetland environments may also favour the development of a novel community of microorganisms that methylate at particularly high rates.

Based on our results, we developed a conceptual model of the biogeochemistry of methyl mercury in a boreal ecosystem consisting of uplands, wetlands, and lakes. Our preliminary precipitation data (Table 5) suggest that precipitation is a source of methyl mercury to the ecosystem, and this source

TABLE 7. Concentrations of mercury in wet deposition and annual inputs of mercury at the ELA and at sites in Scandinavia and North America. In most cases, values represent a range. Single values are means.

Location	Total mercury		Methyl mercury		Reference
	Concentration ($ng \cdot L^{-1}$)	Input ($mg \cdot ha^{-1} \cdot yr^{-1}$)	Concentration ($ng \cdot L^{-1}$)	Input ($mg \cdot ha^{-1} \cdot yr^{-1}$)	
ELA	1.68–5.73	30.8	0.0095–0.028	0.15	This study
Scandinavia					
Denmark	40[a]	170			Iverfeldt 1991a
S. Norway and Sweden	20–35[a]	100–350			Iverfeldt 1991a
S. Sweden				3.0[b]	Hultberg and Iverfeldt 1992
S. Sweden		200			Johanssen et al. 1991
S. Sweden	11–90		0.05–0.59		Lee and Iverfeldt 1991
S.W. Sweden	12–21	120			Iverfeldt 1991b
S. Finland	1.23–2.94	26	0.057–0.093	0.7	M. Verta, personal communication[c]
Central Norway, Sweden, and Finland	10–15[a]	70–130			Iverfeldt 1991a
N. Norway	7–10[a]	30–50			Iverfeldt 1991a
North America					
Little Rock Lake, Wisconsin	Rain: 3.2–15.2 Snow: 6	Rain: 45 Snow: 47.3	Rain: 0.059–0.224 Snow: 0.0–0.08	Rain and snow: 0.88	Fitzgerald et al. 1991
Washington	2–15		0.15–0.35		Bloom and Watras 1989
Dorset	10.2	102			Mierle 1990

[a] Approximate concentrations taken from fig. 7 in Iverfeldt (1991a).
[b] Forest canopy throughfall.
[c] P.B. 250, 00101 Helsinki.

is probably small in remote areas. These data also suggest that as precipitation moves over and through purely upland terrain (such as the U catchment), some of the methyl mercury is either retained or demethylated. When runoff water leaves the uplands and enters wetlands, it picks up methyl mercury produced in the wetlands. Wetlands therefore appear to be important sources of methyl mercury to lakes, which in turn are strong sinks for methyl mercury (yields of methyl mercury from the L catchments were much lower than for any other catchment type (Table 2)).

Our conclusion that wetlands are important sources of methyl mercury does not mean that wetlands are the only important source of methyl mercury to lakes. In seepage lakes, in-lake methyl mercury production is the most important source of methyl mercury (Watras et al. 1994). In the ELA lakes, methyl mercury is produced in the sediments at high rates. For example, fluxes of methyl mercury from sediments of a small lake surrounded by a wetland at the ELA were as high as 10 $ng\cdot m^{-2}\cdot d^{-1}$ during the warm summer months (unpublished data). If this methylation rate occurred only during the warm summer months (approximately 100 d), as shown by previous radioisotopic methylation studies (Ramlal 1983; Winfrey and Rudd 1990), then aquatic methyl mercury production on a per unit basis would be about the same as that for wetland environments. Thus, the relative importance of in-lake versus wetland methylation as sources of methyl mercury to the aquatic food chain would vary according to the area of wetland terrain in a lake catchment. Also, the relative importance of sediment methylation would probably be a function of the water residence time and mean depth of a lake, as has been shown for other sediment microbial activities (Kelly et al. 1987). Clearly, mass-balance studies are needed of inputs and outputs of methyl mercury from lakes together with studies of in-lake rates of methyl mercury production.

Unlike ELA, precipitation appears to be an important source of methyl mercury to watersheds in polluted areas of southern Scandinavia (Table 7). For example, in southern Finland, methyl mercury input by wet deposition is about five times as high as measured at ELA (Table 7). In southern Sweden, Hultberg and Iverfeldt (1992) measured wet and dry deposition of methyl mercury as forest canopy throughfall and found it to be very high (3 $mg\cdot ha^{-1}\cdot yr^{-1}$; Table 7).

While the absolute amount of methyl mercury deposition is much higher in Sweden than at ELA (Table 7), the fate of this methyl mercury in uplands may be similar. In both cases, about 50% of the methyl mercury was retained or demethylated in the upland terrain (Hultberg and Iverfeldt 1992).

Our study is the first to show that methyl mercury is produced at high rates in wetlands. High rates of mercury methylation in wetlands may explain why fish in brown water lakes, which also receive high inputs of DOC from wetlands, have high methyl mercury concentrations (e.g., Meili 1991b).

There are also no other published data showing high methyl mercury retention in drainage lakes. Our estimates of methyl mercury retention in lakes are underestimates because we did not include in-lake methyl mercury production in our study.

Unlike methyl mercury, precipitation was a major source of total mercury to the ELA boreal ecosystem because precipitation inputs were higher than the yields from every type of catchment (Table 5). This conclusion is similar to findings in other areas of North America and Scandinavia (Fitzgerald and Watras 1989; Aastrup et al. 1991; Johansson et al. 1991; Meili 1991b; Mierle and Ingram 1991). Yields of total mercury from the upland (U) and the upland catchments with riparian wetlands (U/W 1 and U/W 2) were quite similar. As water flowed from uplands and into headwater wetlands and then into lakes, progressively more mercury was either volatilized back to the atmosphere or retained (Table 5). In contrast, Mierle (1990) found that a catchment containing wetland areas yielded more mercury than purely upland catchments. Thus, there must be differences among wetlands (e.g., water flow path, acid rain inputs, vegetation, etc.) that affect the degree of mercury retention or volatilization.

Positive correlations between total mercury and methyl mercury concentrations in water have been found from both terrestrial and lake catchments (Lee and Iverfeldt 1981; Meili et al. 1991); however, in our study, there was no relationship (Fig. 5; Table 6). Perhaps the positive correlation in the other two studies, both done in southern Sweden, is related to the much greater importance of both total and methyl mercury in precipitation in that area. This could lead to the percent methyl mercury in runoff being influenced primarily by the percent methyl mercury in precipitation, with only a minor contribution by processes within each watershed. In our area, where methyl mercury concentrations are influenced significantly by within-catchment processes, total mercury was not a good predictor of methyl mercury. Thus, to understand the accumulation of mercury in fish in remote lakes, it is necessary to emphasize the study of methyl mercury as opposed to total mercury.

Acknowledgements

We appreciate the support of the Experimental Lakes Area personnel. We thank A. Bordeleau, J. Hiebert, and M. Lyng for helping with the field sampling and B. Gooding for analytical support. M. Lyng helped collect and prepare the hydrology data. G. McCullough provided tracings of aerial maps for calculations of percent wetland area within each catchment. A. Lynch provided the randomization programs. We thank R.A. Bodaly, R.E. Hecky, A. Heyes, R.H. Hesslein, T. Moore, P.S. Ramlal, N. Roulet, D.M. Rosenberg, J. Shay, and two anonymous reviewers for commenting on earlier versions of this manuscript. We appreciate the financial support of Ontario Hydro, Hydro Quebec, and the Department of Fisheries and Oceans and an NSERC postdoctoral fellowship to V.L. St. Louis.

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Statistical Properties of an Index of Biological Integrity Used to Evaluate Water Resources

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We determined the statistical properties of the index of biotic integrity (IBI) from electrofishing samples collected from Ohio streams. Although IBI is widely used to evaluate the condition of water resources by biologists and resource managers, expanding its role as a regulatory tool depends on statistical validation of its precision and power. We addressed these issues by constructing an additive variance model for IBI and testing the assumptions of that model directly with a bootstrap resampling algorithm and simulations using field data. Statistical properties of IBI supported the use of standard analysis techniques such as ANOVA for hypothesis testing. We determined with power analysis that IBI can distinguish between five and six nonoverlapping categories of biotic integrity based on a model that includes the effects of measurement error, variability of fish assemblages through time, and statistical interaction of location and time. We conclude that IBI is an effective monitoring tool that can be used to communicate qualitative assessments to the public and policy makers or to provide quantitative assessments for a legal or regulatory context based on confidence intervals or hypothesis testing procedures.

Nous avons établi les propriétés statistiques de l'indice d'intégrité biotique (IIB) à partir d'échantillons prélevés par électropêche dans des cours d'eau de l'Ohio. Bien que l'IIB soit largement appliqué à l'évaluation de l'état des ressources en eau par les biologistes et les gestionnaires des ressources, il demeure qu'on doit effectuer la validation statistique de sa précision et de sa puissance avant d'en faire un instrument de réglementation. Nous nous sommes attaqués à ce problème en construisant un modèle de variance additive pour l'IIB et en testant directement les hypothèses à l'origine du modèle en appliquant un algorithme automatique de rééchantillonnage et en faisant des simulations à partir de données sur le terrain. Les propriétés statistiques de l'IIB sont compatibles avec les techniques standard d'analyse telles que l'ANOVA pour la vérification d'hypothèses. Nous avons déterminé par l'analyse de la puissance que l'IIB permet de distinguer entre cinq et six niveaux non superposés d'intégrité biotique à partir d'un modèle qui tient compte des effets des erreurs de mesure, de la variabilité des groupes de poissons dans le temps et de l'interaction statistique entre le lieu et le temps. Nous arrivons à la conclusion que l'IIB est un instrument efficace de surveillance du milieu qui peut servir à communiquer au public et au législateur des évaluations qualitatives ou bien fournir des évaluations quantitatives à des fins réglementaires ou légales, compte tenu de l'application d'intervalles de confiance ou de méthodes de vérification des hypothèses.

Received April 1, 1993
Accepted November 25, 1993
(JB866)

Reçu le 1 avril 1993
Accepté le 25 novembre 1993

The Water Quality Act Amendments of 1972 stimulated new research in state and federal agencies in the United States with the long-term goal of monitoring and assessing the condition of the nation's water resources. At first, resource managers evaluated the condition of rivers and streams according to chemical and physical aspects of surface waters. Use of chemical criteria to define "water quality" and regulate human activities has not provided the protection necessary either to reverse the degradation of rivers and streams (Karr and Dudley 1981; Benke 1990; Hughes and Noss 1992; Allan and Flecker 1993) or to prevent the loss of aquatic species (Miller et al. 1989; Williams et al. 1989; Karr 1992). Traditional approaches based on chemical water quality and sediment toxicity fail to account for other human-induced sources of degradation, such as channelization, introduction of exotic species, and alteration of flow regime (Schlosser 1990; Karr 1991).

Use of biological attributes to evaluate water resources has a long history (Cairns and Pratt 1993). Early approaches (Kolkwitz and Marsson 1908; Chutter 1972; Hilsenhoff 1987) emphasized an organism's tolerance of organic contamination (primarily sewage). Advances in community and population ecology promoted diversity indices (Wilhm and Dorris 1968; Hughes and Gammon 1987) as measures of species richness and evenness, an approach that is largely discredited today (review in Fausch et al. 1990). Recently developed protocols for sample collection and data analysis based on fishes (Karr 1981; Ohio EPA 1988; Lyons 1992) and benthic macroinvertebrates (Lenat 1988; Plafkin et al. 1989; Kerans and Karr, in press) succeed where other

TABLE 1. Biological attributes of fish assemblages used by the Ohio EPA to calculate IBI.

Metric group	Metric	Correlation with degradation
Species composition	1. Total species	Negative
	2. Darter species	Negative
	3. Sunfish species	Negative
	4. Sucker species	Negative
	5. Intolerant species	Negative
	6. % tolerant individuals	Positive
Trophic composition	7. % omnivores	Positive
	8. % insectivores	Negative
	9. % top carnivores	Negative
Fish condition	10. % lithophilic spawners	Negative
	11. % deformed, lesions, tumors	Positive
	12. Total number of fish	Negative

approaches have failed because they integrate the cumulative effects of all human activities, including chemical contamination, and they rely on a quantitative approach founded on ecological theory rather than information theory.

Current US Environmental Protection Agency regulations requiring states to adopt narrative biological criteria in 1993 and numerical biological criteria by 1996 (EPA 1990) reflect the growing recognition that water quality variables alone are not reliable indicators of human influence. As techniques for assessing water resources proliferate (Barbour et al. 1992; Larsen and Christie 1993), quantitative evaluation of the merits of each approach becomes more important. We attempt in this paper to lay the foundation for quantitative comparisons of indices based on their statistical properties, including precision, accuracy, and power. Although these properties are critical for an effective and reliable index, we do not advocate the choice of one biological measurement, or index, over another strictly on the basis of statistical characteristics. Rather, an index should first be judged according to its ability to detect biologically meaningful changes caused by human actions. This paper evaluates the statistical properties of an index of biotic integrity (IBI) developed for use in midwestern streams (Karr 1981; Karr et al. 1986).

Index of Biotic Integrity

IBI is a quantitative assessment tool comprising measurements of 12 biological attributes, termed metrics, of a resident fish assemblage (Fausch et al. 1984; Karr et al. 1986). These metrics quantify biologically meaningful aspects of the fish assemblage that correlate well with human influence, such as species richness and composition, trophic composition, and abundance and condition of fish (Table 1); IBI incorporates ecological information at the individual, population, and assemblage levels. The correlation of IBI scores with human activities is well documented for streams affected by, e.g., sewage treatment (Karr et al. 1985), mine drainage (Leonard and Orth 1986), sedimentation (Berkman et al. 1986), and urbanization and riparian zone destruction (Steedman 1988).

Although different zoogeographic regions support very different faunas, IBI has been successfully adapted for use in numerous North American states and provinces (Leonard and Orth 1986; review in Miller et al. 1988; Steedman 1988; Lyons 1992) because regional reference conditions are used to define expectations. Each metric is assigned a score of 1, 3, or 5 according to whether it deviates strongly, moderately, or slightly from the values observed for reference sites with little or no human influence (Fausch et al. 1984). The overall IBI score for a site equals the sum of the metric scores and can range from 12 (= 12 × 1), indicating a very degraded site, to 60 (= 12 × 5), indicating an excellent site.

Statistical Properties of IBI

To evaluate the statistical properties of IBI, we need (1) a statistical model for IBI and (2) a way to estimate the distribution of the model's error term. The model we use in this paper is an additive response model typically evaluated with the statistical technique known as analysis of variance (ANOVA) whose assumptions provide a framework for evaluating the statistical properties of the response variable IBI. To proceed from model specification to hypothesis testing, underlying assumptions, e.g., bias and homogeneity of variance, must first be verified. Information derived from independent, replicate samples is typically used to verify the assumptions of ANOVA. Repeated measurements of the same sampling unit can result in slightly different values that follow a frequency distribution around the true value. These errors of measurement are included in the statistical model as the residual error term.

One consequence of the way that IBI measures biological integrity is that independent, replicate measurements of a site are not normally available. The sampling protocol used by state and federal agencies to calculate IBI is based on electrofishing which stuns fish at a site so that they can be identified and released. Replicate measurements made the same day or week may not be independent because of the residual effects of the previous electrofishing event; the same is true for other invasive techniques such as seining and trapping. Conversely, measurements made at a slightly different location may be independent but are not true replicates because differences in habitat influence the species found at a site. The best compromise for obtaining independent, replicate measurements would be collecting at the same location at intervals of 2–3 wk. Unfortunately, the expense involved in returning to a site is difficult to justify from the perspective of a regional monitoring program, particularly if those funds could be spent to visit and evaluate another site.

Because IBI scores are based on a single sample, the underlying assumptions of an additive response model are impossible to evaluate from field data alone. Rather than undertake a new study to generate a more ideal data set, we based our statistical analysis and approach on existing data sets. This approach ensures that our results are applicable to current monitoring efforts and allows us to make use of data sets that cover larger geographic areas and longer time periods than we could in an independent project. To test the assumptions for IBI, we can take two alternative approaches: (1) determine or approximate a parametric distribution for IBI and apply the known statistical properties of that distribution or (2) use a distribution-free method, such as a bootstrap resampling algorithm, to estimate the distribution of the error term. The first approach, described briefly below, was less applicable to IBI because of the inherent limitations of nonnormal multivariate statistics. The bootstrap approach was more successful and allowed us to test the assumptions of an ANOVA model for IBI, compare the relative contribution of several sources of variability, and evaluate the precision of IBI.

Methods

Specification of the Model

A general additive response model with IBI as the response variable can be specified as

$$\mathrm{IBI}_{ij} = \mu + \mathrm{site}_i + \mathrm{year}_j + \mathrm{site{\cdot}year}_{ij} + \mathrm{error}_{ij}$$

where IBI_{ij} = observed value of IBI for the ith site in the jth year, μ = overall mean of the response variable, site_i = main effect of the ith location, year_j = main effect of the jth year, $\mathrm{site{\cdot}year}_{ij}$ = interaction effect of the ith site with year j, and error_{ij} = residual error caused by variation in sampling and measurement techniques.

This model includes terms for the effect of location, or site, on IBI score and effects stemming from the time, or year, of measurement. Observed differences in IBI scores within a watershed may result from different levels or types of human influence at the site. Abiotic factors such as rainfall and sunlight may affect patterns of reproduction and mortality that may in turn cause yearly changes in IBI scores. ANOVA tests for the significance of main effects, such as year, by comparing the variance due to year with the residual variance of the error term. The error term for this model, however, lacks a unique subscript, reflecting the fact that only a single observation is available for each combination of site and year.

The model also includes a term ($\mathrm{site{\cdot}year}_{ij}$) representing the interaction of site and year. Interaction can be defined as the observed variance in IBI scores in excess of the variance expected for the combined effects of a particular site and year (Zar 1984). For our model, interaction and error are confounded because of a lack of replicate samples at a site (Hicks 1982), a situation referred to by statisticians as a crossed design without replication. For appropriate situations, interaction may be assumed to equal zero and the confounded term used as an estimate of error. This solution is not acceptable for IBI because we know from empirical evidence that severely degraded sites vary more through time than more pristine sites. One important question to resolve is whether IBI measures real changes in the biotic assemblage (i.e., interaction of time and location is significant) or whether it becomes unreliable at the low end of its range (because of some artifact of the way it is calculated). To resolve this issue, we need to estimate both interaction and error.

Although this model is simple, it is also flexible. More sources of variability can be included by adding terms that would make the model more realistic. For example, the effects of seasonal spawning and migration could be included by adding a term that groups sites according to season. However, because sampling in Ohio was done in late summer/early fall, seasonal variability was effectively eliminated from our analysis. Similarly, the effect of geographic or hydrologic landscape features could be tested by including a term that groups sites according to region. We avoided this source of variability by using data from a single geographic region. As new terms are added to the model to test additional effects, interaction terms quickly accrue: first-order interaction terms for all possible pairs, second-order for all groups of three, and so on. The more complex a model, the more difficult it is to interpret, and consequently, these terms are often included as part of the error term. Yet, ignoring interaction when it is significant can lead to a loss of statistical power, i.e., a loss in the ability to detect differences between sites (Stewart-Oaten 1992). Keeping the model simple by including only two effects, location and time, allowed us to focus on statistical properties of the residual error term.

Error term

The precision of any estimate depends both on the method used to calculate the estimate from data (measurement error) and on the plan of sampling (sampling error). Measurement error is defined as the variability among scores measured at the same site and time; it can be estimated by independently repeating the measurement process on a single sampling unit (Cochran 1977). For IBI, measurement error may arise from diurnal patterns of fish movement that determine which fish are present at the time of sampling; from crew error in identifying fish or transcribing data; or because electrofishing started on the right versus the left bank. The technique used to measure biotic integrity, in this case, electrofishing, introduces additional error. Electrofishing does not capture all fish present, tending to select for larger and less cryptic species (Mahon 1980).

Sampling error is the component of variance due to random sampling variation when n sampling units are measured rather than all N of a population (Cochran 1977). Most documents that refer to biological sampling (e.g., IBI) use the term "sampling" to refer to the process of collecting fish at a site. Although "samples" of fish are collected to estimate the value of IBI, in the language of statistics, fish obtained from a single electrofishing run at a particular site represent a sampling unit. Although fish are identified individually, the level of the measurement is for the entire assemblage; thus the site is the unit of measurement (Hurlbert 1984). A sample, in the statistical sense of the word, refers to the subset of sites chosen from the population of all possible sites within a watershed. The method by which sites are selected from the total population determines sampling error.

Assumptions of the model

Before using any model to compare the relative importance of various sources of variability or to test for significant differences between groups, one must test model assumptions. For simple response variables, such as weight or length, and a simple sampling design, the assumptions of ANOVA are frequently accepted without explicit testing. IBI is a more complex variable derived from several steps of data synthesis; therefore, its assumptions should be tested directly. Testing the assumptions of the statistical model

TABLE 2. Distributional properties of metrics used by the Ohio EPA.

Metric	Approximate range	Type of response
1. Total species	[0, 35]	Integer values
2. Darter species	[0, 9]	Integer values
3. Sunfish species	[0, 6]	Integer values
4. Sucker species	[0, 7]	Integer values
5. Intolerant species	[0, 9]	Integer values
6. % tolerant individuals	[0, 90]	Proportion
7. % omnivores	[0, 60]	Proportion
8. % insectivores	[0, 90]	Proportion
9. % top carnivores	[0, 30]	Proportion
10. % lithophilic spawners	[0, 60]	Proportion
11. % deformed, lesions, tumors	[0, 3]	Proportion
12. Total number of fish	[0, 3000]	Integer values

represents the first step toward hypothesis testing because subsequent statistical inference relies on their being true.

ANOVA makes three primary assumptions about the distribution of the residual error term; its fourth assumption is required only for hypothesis testing (Johnson and Leone 1964): (1) the error term is unbiased, i.e., the expected value of the error term is zero for j repetitions at i sites, or $E(e_{ij}) = 0$, for all i and j; (2) all e_{ij} are mutually uncorrelated among sampling units, i.e., measurement error is not correlated among sites; (3) the variance σ_e^2 is homogeneous for all levels of all treatments; and (4) the distribution of the error term is normal, i.e., e_{ij} has a normal distribution with mean 0 and variance σ_e^2. Although we show the general case with only two subscripts for the error term, all assumptions would apply to any source of variability subscripted in the error term.

Classical statistics instructs us to test these assumptions by taking repeated independent, random measurements of IBI for all levels of the factors of interest to estimate the measurement error, or pure error, of the response variable itself, in this case, IBI. Unfortunately, repeated random measures are not possible (1) because of the time and space effects already described, (2) because agency budgets may not permit sufficient sampling, and (3) because the time before water resource decisions must be made is often limited. Thus, the distribution of the error term cannot be determined from field data and therefore must be derived analytically from a known parametric distribution or estimated using the bootstrap method to resample from the original data.

Parametric Approach

Calculating an IBI score from electrofishing data requires evaluating metrics, assigning scores to metric values (1, 3, or 5), and summing scores to get an overall IBI. To determine a parametric distribution for IBI scores at a site, we began with the distributional properties of the 12 metrics. All 12 metrics are calculated from a single electrofishing sample; they are therefore not independent and require a multivariate model to account for correlation among metrics.

We first considered using the multivariate normal distribution because the mean, variance, and covariance are easily calculated from the univariate distributions. The total number of fish (metric 12) has a broad range of possible values and could potentially be modeled as a normal random variable (Table 2). Furthermore, proportional IBI metrics (metrics 6–11) could be transformed to stabilize variance and approximated by a normal distribution. But metrics 1–5 are species counts, and their narrow range makes them too discontinuous to be accurately modeled by a normal curve.

When a random variable takes on discrete, integer values, the appropriate distribution is the Poisson if the mean and variance are approximately equal, or the negative binomial when the variance is greater than the mean (Elliott 1977). The multivariate Poisson has several undesirable properties, however: the mean and variance must be equal, covariance between two metrics is restricted to be smaller than the smallest mean of the two metrics, and marginal and conditional distributions cannot both be modeled with another Poisson distribution (Haight 1967). Although the negative binomial distribution does not assume equal mean and variance, properties of the multivariate negative binomial distribution are not well known.

Finally, we considered a multinomial distribution: metrics 2, 3, and 4 could potentially be modeled as a multinomial distribution with parameters for the relative proportions of darter, sunfish, sucker, and other species. Correlation between metrics is part of the model, although restricted to only negative values. Such a restriction was unreasonable because the three fish taxa are influenced by different sources of degradation; therefore, correlation among them may be positive or negative.

Thus, underlying distributional differences among the 12 IBI metrics (see Table 2) limited the applicability of parametric distributions. The degree of approximation involved in forcing IBI to any of the previous distributions suggested that nonparametric approaches would be more appropriate.

Bootstrap to Estimate Measurement Error

The bootstrap algorithm is most often used to determine the confidence interval of a test statistic for which the actual distribution is unknown (Efron 1981). Bootstrapping is particularly useful when only a single random sample exists. In the case of IBI, a single electrofishing sample provided data to calculate a single IBI score, and without replicate samples, a confidence interval for a site could not be estimated. Other algorithms, e.g., the jackknife, are asymptotically equivalent to the bootstrap but, in general, do not perform as well for estimating variance (Efron and Gong 1983). Other applications of the bootstrap to data on species abundance include estimating confidence intervals for a similarity index (Smith et al. 1986) and comparing clustering techniques (Nemec and Brinkhurst 1988).

The bootstrap algorithm creates new samples by resampling from an original random sample. Elements are chosen at random from the original sample and replaced; thus, each element may be selected more than once or not at all. Random sampling with replacement continues until the bootstrap sample contains the same number of elements as the original sample. The test statistic of interest (mean, correlation coefficient, etc.) is calculated for each bootstrap sample and saved. For IBI as test statistic, imagine a large tank containing all the fish collected at the original field site. An individual fish is chosen from the tank at random, identified, and then replaced where it has the same probability as every other individual in the tank of being chosen the next time. One repeats this process and then estimates the test statistic for each new sample until enough values for IBI have accumulated to approximate its distribution at a site. The result is the distribution of the error term that we need to test the assumptions of the statistical model for IBI; it can be expressed as (Cochran 1977)

$$\mathrm{IBI}_{ij} = \mu_i + e_{ij}$$

where IBI_{ij} = IBI value at the ith site on the jth repetition, μ_i = true value of IBI at the ith site, and e_{ij} = error of measurement at the ith site on the jth (bootstrap) repetition.

For the ith site, the bootstrap algorithm generates j repetitions, which provide a distribution for the error term from actual data. From the distribution of bootstrap IBI scores at a site, a confidence interval can be calculated to estimate the amount of variability in these scores due to measurement error, i.e., variability built into IBI and not caused by changes in the resident fish assemblage. For 100 rank-ordered bootstrap IBI scores, the fifth ordered value represents the lower bound of a 90% confidence interval, and the ninety-fifth ordered value represents the upper bound. The number of bootstrap scores should be large enough to ensure that results are independent of the random seed that initializes the bootstrap process. In our case, 500 bootstrap samples provided a stable distribution for IBI scores at a site.

Limitations and assumptions of the bootstrap

Although the bootstrap algorithm makes no parametric assumptions, the original sample from which subsequent bootstrap samples are created is assumed to be truly random. IBI protocol also assumes that fish are collected in true relative abundance without bias toward taxa or size (Karr et al. 1986). In other words, both the bootstrap algorithm and IBI assume that selectivity of gear produces no bias and that biologists are well trained in identifying all species collected. Studies with rotenone, however, indicate that electrofishing misses small and cryptic species and therefore does bias which fish are selected (Mahon 1980). A subsequent analysis of the same data found that IBI was not greatly altered by adding the missed species (Steedman 1988).

The distributions generated by the bootstrap algorithm of IBI scores at a site do not include all possible sources of variability, in particular sampling error resulting from spatial heterogeneity of species distributions. We did not intend to extend our conclusions about score variability to the larger population of sites within a whole watershed; rather, we concerned ourselves primarily with testing the behavior of IBI as a measurement tool for evaluating the biotic integrity of a site from electrofishing data. The sample used in the bootstrap analysis was the collection of fish obtained by electrofishing at a site; although fish are collected, the site is being measured. The population to which we draw inference is still the site; but bootstrap samples represent collections of fish that could have been caught at the same site and time by electrofishing. Not all species present at a site need be collected by the original electrofishing event because IBI is designed to be robust to that source of measurement error. For example, the metric for total number of species (see Table 1, metric 1) is scored as a 5 whether 24, 25, or 35 species are recorded.

All metric values and scores calculated from bootstrap samples varied, with one exception: total number of fish (metric 12). Without field data to estimate the distribution of this metric, we left it as a constant equal to the number of fish in the original sample; thus, our analysis may have underestimated IBI's overall variance. Allowing metric 12 to vary would have a pervasive effect on all other metrics because metric 12 determines the number of fish in each bootstrap sample. One solution would be to use a smoothed bootstrap to sample from a Poisson distribution with the variance and mean equal to the observed number of fish. This method would estimate only a *lower* bound of the variance because abundance data typically show variance greater than the mean; in such a case the negative binomial distribution is more appropriate (Elliott 1977). We feel that this approach extrapolates beyond the data, however, in that it assumes that the relative proportions of fish species stay the same in large or small collections.

Study Sites and Data Collection

The Ohio Environmental Protection Agency has collected data for assessing water resource quality since the late 1970s. The agency strictly defines data collection techniques for biological criteria and applies them consistently for all regions within the state (Ohio EPA 1988), making the resulting data set ideal for exploring the statistical properties of IBI. Fish at a site were collected using electrofishing gear which stuns fish so they can be counted, identified to species, checked for anomalies such as tumors or lesions, and then released.

Ohio includes five geographic regions: the Eastern Corn Belt Plains, the Huron – Erie Lake Plain, the Erie – Ontario Lake Plain, the Western Allegheny Plateau, and the Interior Plateau. Within each region, three size classes of rivers and streams are recognized and sampled with slightly different gear. Scoring criteria differed slightly depending on geographic location and stream size. Our analyses included sites within Ohio's Eastern Corn Belt Plains ecoregion with a drainage area of between 20 and 300 mi^2. We analyzed data for sites from three river basins: Great Miami (n = 37), Maumee (n = 18), and Sandusky (n = 12). These sites were sampled with portable electrofishing gear from bank to bank for 200 m along the channel in late summer/early fall from July to October 1980–90.

Because much of our statistical analysis could be considered exploratory, we divided the data into two parts. We tested conclusions based on results for the Great Miami Basin (the "exploratory" data set) with data from the Maumee and Sandusky basins to ensure their validity. For this second data set, we used one-tailed tests because only results that agree with the first data set indicate a significant relationship that can be generalized to a larger population of all sites. Significant correlation in the opposite direction would rep-

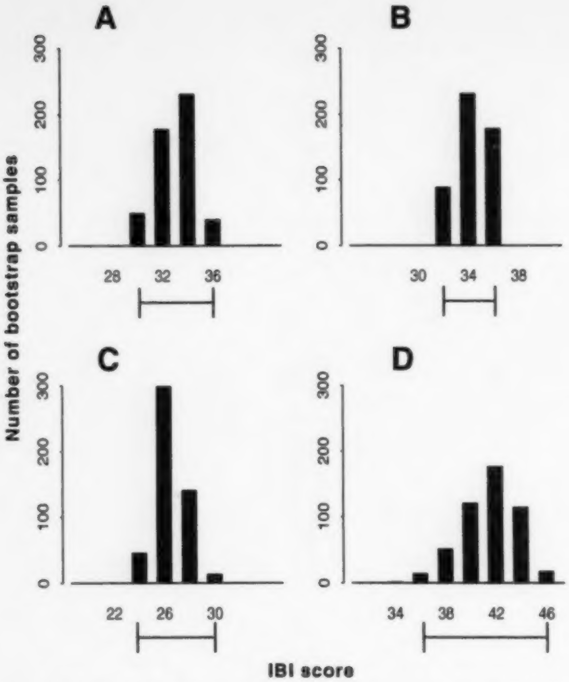

FIG. 1. (A–D) Distribution of bootstrap IBI scores at four typical field sites. Spread of the distribution represents measurement error. The 95% confidence interval is shown below the *x*-axis.

resent a contradictory result from which we would conclude that correlation was specific to the data set and not meaningful in a broader context.

Results

The distribution of bootstrap IBI scores at a site provided the independent, repeated measurements needed to test the assumptions of an additive response model for IBI. After verifying the first three assumptions of ANOVA, we estimated interaction and error separately. We then ran simulations incorporating field data to test the fourth assumption and estimate the statistical power of IBI.

Distribution of IBI Scores at a Site

Generally, the distributions of IBI scores at a site were unimodal with short tails (Fig. 1). Asymmetry of the distribution indicates bias. The first assumption of ANOVA is that the measurement error is unbiased, i.e., $E(e_{ij}) = 0$. Recall that the model for the distribution of the error term at the ith site is

$$\mathrm{IBI}_{ij} = \mu_i + e_{ij}.$$

We took the "true" IBI value for a site μ_i as the value calculated for the original field sample. We then estimated bias, B_i, by subtracting the true value from the mean of the bootstrap IBI values for the ith site; a result other than zero indicated bias:

$$B_i = \overline{\mathrm{IBI}}_{\mathrm{BS}} - \mu_i.$$

Using this method, we found that bootstrap IBI scores for 37 sites within the Great Miami basin were significantly

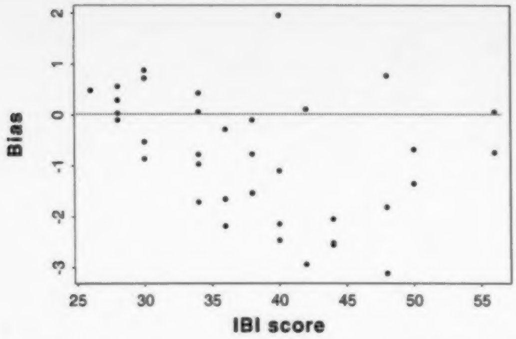

FIG. 2. Bias of measurement error plotted against IBI score showing negative correlation and bias of measurement error toward negative values ($n = 37$, Great Miami basin).

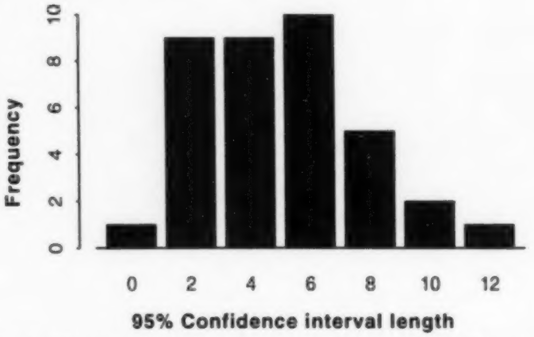

FIG. 3. Histogram of confidence interval lengths for IBI scores; the *x*-axis is the length and the *y*-axis records the frequency of occurrence ($n = 37$, Great Miami basin).

lower than the score calculated from the original field data ($t = -4.05$, $p < 0.05$). Although a majority of sites showed this pattern, not all did; bootstrap IBI scores for sites with low IBI scores tended to be higher (Spearman's $\rho = -0.42$, $p < 0.01$, two-tailed test; Fig. 2). Similar results were obtained for 30 sites in the Maumee and Sandusky basins ($t = -2.3$, $p < 0.05$), although the negative correlation between IBI scores and bias was not as strong ($\rho = -0.33$, $p < 0.05$, one-tailed test). Bootstrap IBI scores tended to be higher than the true scores for sites with low original scores and lower for sites with high original scores. In other words, biotic integrity tends to be overestimated for degraded sites and underestimated for more pristine sites.

Correlation of Measurement Error within Sampling Units

For sampling units (sites) within the Great Miami basin, 95% confidence interval lengths ranged from 0 to 12 (Fig. 3), and only 8 of the 37 sites had confidence intervals greater than 6. The second assumption of ANOVA requires measurement error to be uncorrelated among sampling units, or sites. Translating this assumption into a testable hypothesis, we wanted to know whether sites with large confidence intervals were predicted by some characteristic of the site or sample.

Small numbers of individual fish in original field collections were correlated with high measurement error (Spearman's $\rho = -0.50$, $p < 0.01$; Fig. 4). For Great Miami basin, seven of eight sites with confidence intervals greater

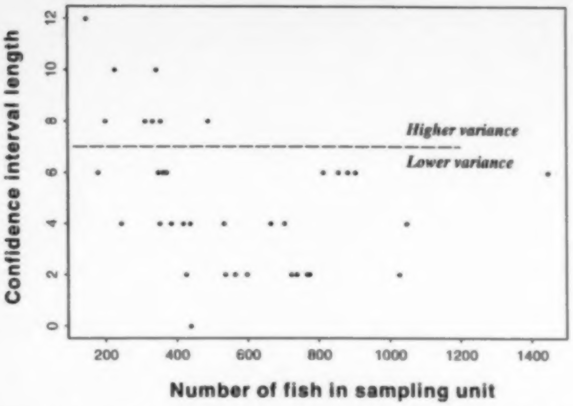

FIG. 4. Confidence interval length of IBI plotted against the number of individuals collected at a field site ($n = 37$, Great Miami basin).

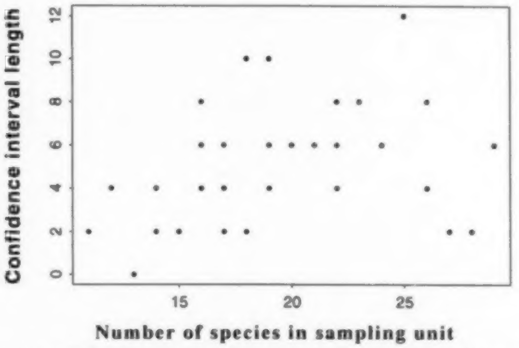

FIG. 5. Confidence interval length of IBI plotted against the number of species in a collection ($n = 37$, Great Miami basin).

than 6 had fewer than 400 individuals in the sample. Similarly, for the Maumee and Sandusky basins, sites with small numbers of fish had wider confidence intervals ($\rho = -0.58$, $p < 0.01$) and five of eight sites with confidence intervals greater than 6 had less than 400 individuals.

Bootstrap IBI scores for sites with a small number of species were less variable ($\rho = 0.38$, $p < 0.05$; Fig. 5). However, the relationship did not extend beyond about 15 species and was not significant at all for Maumee or Sandusky sites ($p > 0.05$).

Homogeneity of Variance

ANOVA assumes that variance is homogeneous across the range of the response variable; therefore, measurement error and IBI score should be independent. The length of the confidence interval and median IBI were not significantly correlated for either the Great Miami basin ($p > 0.05$; Fig. 6) or the Maumee and Sandusky basins. We therefore concluded that measurement error was homogeneous across the possible range of IBI scores.

Interaction

We had two methods available for estimating variance of IBI scores at a site: (1) replicate samples taken through time and (2) bootstrap samples. The Great Miami data set included nine sites measured at three different times during the same year. The variances calculated from replicates through time were correlated with IBI scores ($\rho = -0.60$; $p < 0.05$), but bootstrap estimates of variance were not. A comparison of these two estimates of variance revealed that for more pristine sites (high IBI scores), the two estimates were in close agreement (Fig. 7), but for degraded sites, another source of variability was affecting the scores over time. This source of variability was the statistical interaction of time and location.

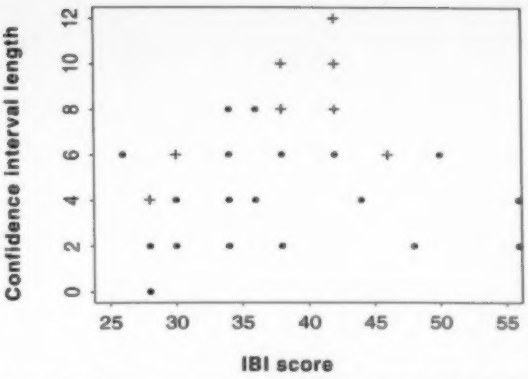

FIG. 6. Confidence interval length of IBI plotted against median IBI score ($n = 37$, Great Miami basin). Pluses denote small (<350) numbers of fish in the original collection.

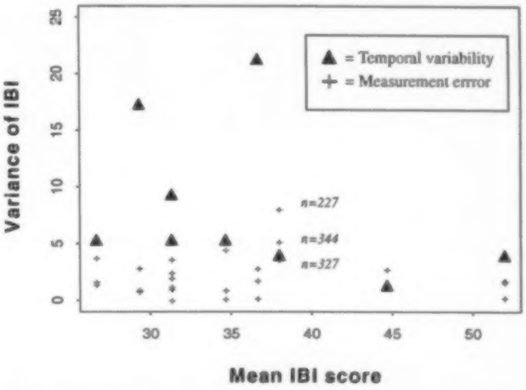

FIG. 7. Mean IBI score plotted against the temporal variance (triangles) and measurement error (pluses) for nine sites in the Great Miami basin sampled at three different times. The number of fish in the sampling unit is shown for one location with particularly high measurement error.

Although residual error and interaction were confounded for the ANOVA model, using the bootstrap samples, we could estimate all the terms of the model (Table 3). Not surprisingly, differences due to *location* explained most of the observed variability of IBI scores. The very small contribution of *time* to overall variability indicated that sampling during late summer/early fall effectively minimizes temporal variability. Interaction of *location* and *time* was a larger component of variance than *time* alone or residual error.

IBI scores for less-degraded sites at different times agreed closely and were therefore more consistent than scores for

TABLE 3. ANOVA of IBI scores for nine sites within Great Miami basin, Ohio, at three times within a year.

Source of variation	df	Mean square	Expected mean square[a]
Main effects	10		
Location, s_i	8	192.1	$\sigma_e^2 + \sigma_{ST}^2 + 3\sigma_S^2$
Time, t_j	2	7.3	$\sigma_e^2 + \sigma_{ST}^2 + 9\sigma_T^2$
Two-way interaction, st_{ij}	16	8.2	$\sigma_e^2 + \sigma_{ST}^2$
Residual, e_{ij}	0	2.2[b]	σ_e^2
Total	26		

[a] $\hat{\sigma}_S^2 = 61.3$, $\hat{\sigma}_T^2 = 0$, $\hat{\sigma}_{ST}^2 = 6.0$, $\hat{\sigma}_e^2 = 2.2$.

[b] Estimated from bootstrap distributions.

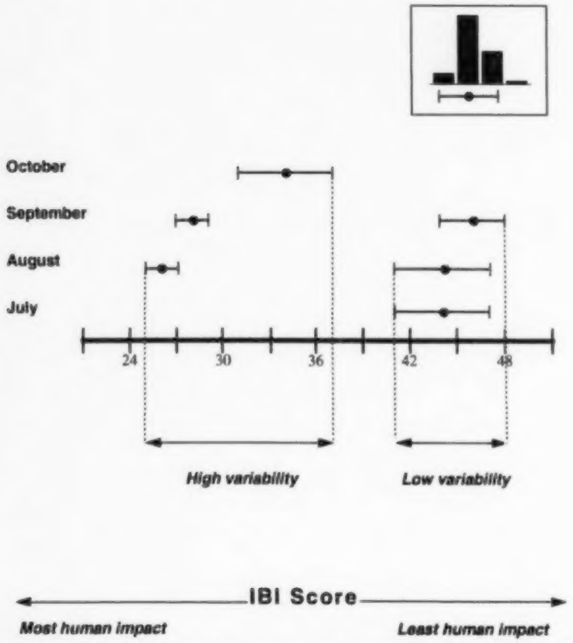

FIG. 8. Contribution of measurement error and temporal variability to the overall variance of IBI at two locations (grouped by broken lines), sampled on three occasions. Error bars represent the 95% confidence interval calculated from bootstrap sampling (see inset for example).

disturbed sites (Fig. 8). Although measurement error may be lower for a more disturbed location, that fact alone cannot compensate for the high overall variability of the IBI score.

Distribution of the Test Statistic under the Null Hypothesis

For hypothesis testing, the last assumption of ANOVA requires the error term to be distributed as a normal random variable. Two points suggest that this assumption was not unreasonable for IBI: (1) the distribution of the measurement error tends to be unimodal (see Fig. 1) and (2) IBI is the sum of 12 random variables. By the central limit theorem, the distribution of a mean (or sum) of random variables converges toward a normal distribution as the number of variables increases toward infinity (Casella and Berger 1990). We used simulation to test this assumption directly.

TABLE 4. Simulation results comparing the test statistic calculated under the null hypothesis with the *t*-distribution. Reported empirical values are averages for 15 sampling units.

$n_1 = n_2$	df	α-level	*p* (empirical)
5	8	0.01	0.012
5	8	0.02	0.018
5	8	0.05	0.049
5	8	0.10	0.097
10	18	0.01	0.010
10	18	0.02	0.019
10	18	0.05	0.045
10	18	0.10	0.098
15	28	0.01	0.009
15	28	0.02	0.020
15	28	0.05	0.049
15	28	0.10	0.098

Imagine a simple scenario in which one site has a sewage outflow and a similar site does not. To test whether the sites are different, one could compare replicates with a *t*-test. In this case, the distribution of the test statistic under the null hypothesis is assumed to be a Student *t* distribution. One decides whether to accept or reject the null hypothesis (that the sites do not differ) according to where the *t*-value falls in this distribution. If our simulations produce *t*-values that reject the null hypothesis too often, we would conclude that the fourth assumption is not verifiable for IBI.

For our simulations, we made sure that the null hypothesis was true by creating bootstrap samples from a single field site and assigning them randomly to two groups. The test statistic was calculated as

$$t = \frac{\overline{\mathrm{IBI}}_1 - \overline{\mathrm{IBI}}_2}{\sqrt{S_p^2\left(\frac{1}{n_1}+\frac{1}{n_2}\right)}}$$

where $\overline{\mathrm{IBI}}_i$ = average IBI value in the *i*th group, S_p^2 = pooled variance, and n_j = number of bootstrap samples in each group. A distribution for *t* was approximated by creating enough bootstrap samples to calculate 500 values of *t*.

Although the overall shapes of the empirical and theoretical distributions were nearly identical by visual inspection, we took a closer look at the tails because that is where the null hypothesis is rejected. The percentage of empirical test statistics greater than $|t_{\alpha,df}|$-values was compared with the α-level expected for the Student *t* distribution. Distributions were compared for 15 field sites using bootstrap sample sizes of 5, 10, and 15 for each group (Table 4). Excellent agreement between the α-level and the empirical *p*-value indicated that the null hypothesis was rejected at about the same rate as expected for the *t* distribution.

Power Analysis

Statistical power is defined as the probability of rejecting the null hypothesis when it is false. Power measures IBI's ability to distinguish between locations that are indeed different. Much as $\alpha = 0.05$ is an accepted standard for the risk of type I error (rejecting the null hypothesis when it is true), power equal to 80% is a widely used standard (Peterman 1990).

We used the *t*-test described above to compare sites, except this time, we compared different sites; thus the null hypothesis was false. For nine field sites, there were 36 possible pairwise comparisons. We again used the bootstrap to generate replicate samples, but instead of generating all the bootstrap samples from one original field sample, one bootstrap sample was created from each of three sampling occasions at each site. Thus, power analysis included measurement error (estimated by the bootstrap) as well as temporal variability and interaction (estimated by replicates through time). For each pair, bootstrap samples were generated and sites were compared 500 times. For all 36 pairs, power was calculated as the percentage of *t*-values that rejected the null hypothesis.

Our results showed that IBI could reliably detect differences in sites when mean scores differed by more than 8.5 points for standard values of α and β (Fig. 9). Another way to express this result was in terms of the number of distinct classes of biotic integrity that IBI can distinguish. IBI scores range from 12 to 60; dividing the difference, 48, by 8.5 yielded five to six classes. Although we had been concerned that the relatively large amount of variance due to interaction (see Table 3) could adversely affect IBI's power, we concluded that power was sufficient to distinguish biologically meaningful differences in the resident fish assemblage.

Discussion

Our goal was to evaluate the precision of IBI, a measurement tool used to evaluate stream condition. The bootstrap algorithm provided replicate samples from which we could calculate variability among scores at a site. This variability, which we refer to as measurement error, is a consequence of the protocol that converts electrofishing data into a measurement of biotic integrity. In addition, we tested other statistical properties of IBI to verify that an additive response model is appropriate for comparing the relative contribution of different sources of variance. Finally, simulations demonstrated that IBI has sufficient power to detect meaningful biological change in a formal hypothesis testing framework.

Homogeneity of Variance

Of particular concern for IBI was the observed correlation between its mean and variance reported from field studies (Karr et al. 1987; Steedman 1988; Yoder 1991). IBI scores for more pristine sites vary less than scores at degraded sites. Two possible explanations for this relationship are that (1) IBI scores reflect real changes in the resident biota and (2) the process that converts electrofishing data into IBI scores introduces a statistical artifact. Repeated measurements through time are usually the only data available to estimate variance at a site; without replicates for each time point, a distinction between temporal variability and measurement error cannot be made. Using a bootstrap algorithm, we estimated the variance of IBI at a site independent of time and were able to demonstrate that a significant effect beyond the additive effects of time and location contributes to score variability. Because this additional effect was not a statistical artifact, we attribute it to the statistical interaction of time and location.

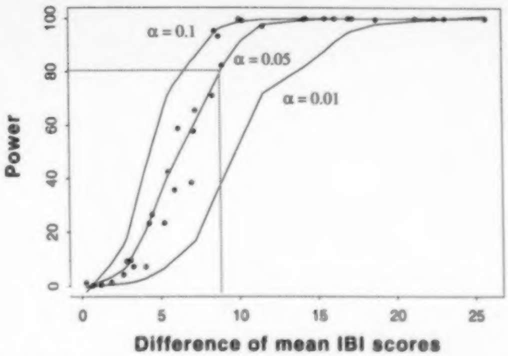

FIG. 9. Power curves for IBI estimated from nine locations sampled three times. Actual points are shown only for $\alpha = 0.05$; other values of α are pictured as smoothed lines.

The high variability of IBI scores from degraded sites reflects biological changes in the resident assemblage. Biological systems subject to a high level of human disturbance are less resilient to abiotic changes occurring as a result of natural processes. Behavioral strategies, such as local migration, that have evolved in response to "normal" levels of stress caused by floods or temperature extremes cannot compensate for the higher levels of human-induced disturbance. Disturbed systems have essentially lost their capacity to buffer normal changes (Toth et al. 1982). For Ohio streams, high variability of IBI scores may be an early-warning sign of increasing human influence. This relationship must be tested before being applied to streams in other regions, however; in western streams, for example, human influence may actually increase stability (Bramblett and Fausch 1991).

Independence of Sampling Units

Covariance among measurement error terms for different sites is analogous to "interviewer bias" for questionnaire sampling (Cochran 1977). Interviewer bias refers to the effect an interviewer may have on the person being questioned (e.g., encouraging them to give certain answers). For IBI, if variance at a site correlates with a characteristic of the site or sampling technique, measurement error for those sites is said to be correlated. IBI scores at sites for which less than 400 fish were collected were notably more variable. Smaller sample sizes provide less information and, consequently, are more variable. This lack of information was a consequence of neither the sampling protocol nor the bootstrap algorithm but an inherent feature of the site. Because the same level of sampling effort was used at each site, the number of fish collected is therefore a characteristic of the site itself and not caused by the sampling or resampling procedure and (to a certain extent) determined the variance associated with it. Bootstrapping cannot overcome limitations of the original sample collected, nor can it extrapolate beyond the data at hand. The obvious break at 400 individuals indicates that the amount of gain in precision beyond 400 is less important than the loss below 400. Standardized sampling protocol should specify a large enough area to ensure that most sites yield at least 400 individuals. For extremely degraded sites, this number may be impossible to obtain. This result may also be of practical concern for zoogeographic regions or stream sizes that naturally support few fish.

Bias

For IBI, bias is systematically related to the value of IBI itself: IBI scores calculated from actual electrofishing data had higher bootstrap scores when the true score was low and tended not to go below a threshold of 20. At the other end, sites with high IBI scores yielded lower bootstrap scores up to a threshold of approximately 45, beyond which the relationship was not observed. This tendency of bootstrap scores to fall closer to the middle of their possible range may lead to underestimation of differences between sites.

Correlation of bias with score also suggests an explanation for the bias (see Fig. 2). Scoring metrics as 1, 3, or 5 means that for pristine sites, a good number of metrics score a 5; when we varied the samples with bootstrapping, metric scores could only decrease to a 1 or 3. On the other hand, for degraded sites with a good number of metrics scored as 1, bootstrap metric scores can only improve to a 3 or 5. Bias is thus a consequence of the way metric values are discretized into scores. Scoring based on more categories, e.g., 1, 3, 5, 7, 9, would probably reduce this source of bias.

In a monitoring context, bias may cause the quality of degraded sites to be overestimated and good sites to be underestimated. This bias is an inherent feature of IBI and results from the number of categories used to divide the range of the metrics. The worst-case scenario is that differences between sites will be underestimated. Until the current ability of IBI to discriminate differences in biotic integrity is judged inadequate, we do not recommend changing the protocol currently in use because the effects of the bias are small.

Extending the Model for Hypothesis Testing

Our simulations indicate that although IBI scores at a site are not distributed normally, the test statistic calculated to compare sites closely approximates that of the expected t-distribution. Because a two-sample t-test is mathematically equivalent to an F-test in ANOVA when comparing two groups, results for two-sample t-tests may be cautiously applied to a full ANOVA model. The fact that a simple and familiar statistical model is appropriate for IBI means that statistical software available to most resource managers can be used to compare sites, and the status of and trends within watersheds can be communicated without invoking more complex statistical models.

With a statistical model in place, the next step was to test the ability of IBI to distinguish between sites, given two inherent sources of variability: measurement error introduced by the measurement process itself and the natural variability of the biota due to the effects of time. It is important to distinguish between variability caused by measurement error and variability caused by the effects one is interested in monitoring. If measurement error is small relative to the effects being monitored, then the measurement tool is sufficiently precise. The very small effect of time and the small relative contribution of measurement error to the overall variance (see Table 3) indicate that IBI is an effective management tool capable of detecting biologically meaningful change resulting from natural causes or human influence. The high precision of IBI is a consequence of sampling protocols that minimize the effects of seasonality and the accuracy of the individual component metrics included in the index.

Monitoring versus Hypothesis Testing

Hypothesis testing is an appropriate assessment tool when a specific evaluation of known problems is required. Nevertheless, management decisions are rarely made on the basis of a p-value. In a decision-making context, the important questions concern the extent of human-induced changes and our precision in estimating them (Stewart-Oaten et al. 1992). In addition, the potential number of statistical comparisons is very large, but the results of those tests may not be useful for monitoring or detecting trends in biotic integrity. For both situations, confidence intervals can be used to express the uncertainty associated with estimates of biotic integrity; they provide the guidelines to judge the significance of observed changes in IBI scores.

A more practical expression of diagnostic power lies in terms of standard deviation and the number of qualitative categories of biotic integrity that IBI can distinguish. Using repeated measurements through time at a site, the standard deviation of IBI scores was previously reported as approximately ±4 (Angermeier and Karr 1986; Karr et al. 1987). Bootstrapping excluded the effects of time when estimating the standard deviation at a site and therefore provided a smaller estimate of ±3 and closer to ±2 for sites with more than 400 fish collected. Field samples collected at different times at sites experiencing no new human influences led to the definition of five quality classes from excellent to very poor (Karr et al. 1986; Ohio EPA 1988). Conventional usage of five classes agreed closely with the results of our power analysis, which indicate that IBI can reliably distinguish five to six categories when replicates through time are used. We conclude that IBI is an effective monitoring tool for evaluating the effects of human influences on rivers and streams in Ohio, whether reporting confidence intervals, testing specific hypotheses using familiar statistical procedures such as ANOVA, or providing qualitative assessments based on five classes of biotic integrity.

Acknowledgments

Ed Rankin and Chris Yoder of Ohio EPA provided the data used in these analyses. This research was supported in part by a grant from the Tennessee Valley Authority to James R. Karr.

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A 50-yr Record of Pollution by Nutrients, Trace Metals, and Organic Chemicals in the St. Lawrence River

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The deposition chronology of algal pigments, organic C, N, P, trace metals, and organic contaminants (PCB congeners, DDD, DDE, Mirex, hexachlorobenzene) is described for two sites in fluvial lakes (St. Francis and St. Louis) of the St. Lawrence River. Pigment concentrations rapidly decrease in the top 10 cm due to degradation, but show a broad secondary peak consistent with higher primary productivity between 1960 and 1975. In Lake St. Francis, deposition of organic C, N, and P peaked between 1950 and 1975. In both lakes, trace metal concentrations reached maximum values between 1960 and 1970 and decreased considerably between 1970 and 1980. At both sites, surficial trace metal concentrations are approaching (within a factor of 3) those observed in preindustrial sediments except Cd, which is still 5–6 times higher. Concentrations of Cr, Cu, Ni, and Zn are inversely related ($p < 0.05$) to river discharge whereas those of Pb are positively related to discharge. Concentrations of organic contaminants have declined by a factor of 5–10 between the mid-1960's and the early 1980's, except Mirex, which shows no obvious trend with time. Historic trends in pollution by organic chemicals appear to have been influenced not only by changing anthropogenic inputs, but also by river discharge.

Nous décrivons la chronologie de sédimentation des pigments algaires, du C organique, du N, du P, des métaux-traces et des contaminants organiques (congénères de BPC, DDD, DDE, Mirex, hexachlorobenzène) à deux stations dans les lacs Saint-François et Saint-Louis, sur le Saint-Laurent. Dans les 10 premiers cm de sédiments, la concentration en pigments diminue rapidement par décomposition, mais on observe un large pic secondaire qui correspond à une production primaire accrue entre 1960 et 1975. Dans le lac Saint-François, la sédimentation du C organique, du N et du P est passée par un maximum entre 1950 et 1975. Dans les deux lacs, la concentration en métaux-traces a atteint un maximum entre 1960 et 1970, pour décroître considérablement entre 1970 et 1980. Aux deux stations, la concentration en métaux-traces à la surface s'approche (par un facteur de 3) de la concentration observée dans les sédiments préindustriels, exception faite du Cd qui reste 5 à 6 fois plus abondant. La concentration en Cr, Cu, Ni et Zn est en proportion inverse ($p < 0,05$) du débit du fleuve alors que celle du Pb est en corrélation positive avec le débit. La concentration en contaminants organiques a diminué par un facteur de 5 à 10 entre le milieu des années 1960 et le commencement des années 1980, sauf pour le Mirex auquel aucune tendance claire dans le temps n'est associée. Les tendances historiques de la pollution par des composés chimiques organiques paraissent avoir été marquées non seulement par les apports d'origine anthropique, mais aussi par le débit du fleuve.

Received July 16, 1993
Accepted November 26, 1993
(JC011)

Reçu le 16 juillet 1993
Accepté le 26 novembre 1993

Since the beginning of the century, urban, industrial, and agricultural development has caused a deterioration of water quality in the Great Lakes and in the St. Lawrence River. During the last 20 yr, substantial efforts have been made to reverse this trend by reducing P loading (Vallentyne and Beeton 1988; International Joint Commission 1991, 1992) and limiting or phasing out the use of some persistent organic contaminants. More recently, additional measures have been taken to further reduce point sources of contaminants in the St. Lawrence (Government of Canada 1991). The effects of some remedial measures, such as P loading reductions, have been directly monitored in the Great Lakes since 1968. Similar information is lacking, however, for the great majority of contaminants that have been introduced in the St. Lawrence since the beginning of the industrial age. Thus, we currently have little information on the previous contamination state of the system and on its response to past and present efforts to reduce contaminant loading. Sedimentary records are frequently used to infer the history of anthropogenic effects in aquatic systems when direct observations are lacking. In Lake Ontario, the nearest system for which sedimentary records are available, cores collected near the mouth of the Niagara River have revealed clearly decreasing contamination levels after the mid-1960's (Durham and Oliver 1983). In other parts of the lake, however, sediment chronologies have been more ambiguous (e.g., Oliver et al. 1989) due to typically low sedimentation rates and to the blurring effect of bioturbation.

During a previous study on the sediment dynamics of the St. Lawrence (Carignan et al. 1994), we have encountered two sites where local conditions have allowed an exceptional preservation of past contamination trends in the sediments. Dated cores taken at these sites are described here to provide a broad picture of the physical, biological, and chemical changes that have taken place during the last 50 yr.

Study Site

Between 1932 and 1941, flow between the two fluvial lakes St. Francis and St. Louis was progressively diverted through the Beauharnois canal for power generation (Fig. 1). As a result, fine-grained sediments began to accumulate rapidly (1–2 $cm \cdot yr^{-1}$) in deeper parts of the former natural river channel located in the northeastern section of Lake St. Francis and in western Lake St. Louis. Because sedimentation rates are high at these sites, the blurring effect of biological/physical sediment mixing is relatively small, and past changes in sediment quality have left clear signals. Each fluvial lake of the St. Lawrence can be viewed as two independent lateral water masses separated by the main channel through which most (70–90%) of the river passes directly with little interaction with the lateral sections. The two stations are influenced by different hydrological and physicochemical conditions that may affect pollutant deposition and concentrations in their sediments.

Station SL-28 (45°14.60′N, 74°11.54′W, depth = 6.7 m) is located at the downstream end of the northern section of Lake St. Francis (Fig. 1). This water mass has an estimated mean residence time of about 12 d (Carignan et al. 1994), a mean depth of 5.1 m, and a relatively high water transparency that allows abundant macrophyte and associated periphyton growth (e.g., *Vallisneria americana*, *Myriophyllum spicatum*, *Potamogeton richardsonii*, *Chara* sp.) over approximately 90% of the bottom area. Submersed vascular macrophytes occupy the 0.5- to 5-m zone whereas 20- to 30-cm-thick *Chara* meadows tend to cover deeper (5–6 m) areas. No macrophytes were present at station SL-28 at the time of sampling. Based on the average light extinction coefficient ($0.5 \cdot m^{-1}$) reported for the northeast section of Lake St. Francis (B. Pinel-Alloul, Sciences biologiques, Université de Montréal, Montreal, QC H3C 3J7, personal communication), the bottom sediment at SL-28 presently receives about 3.5% of the incident light. Bottom sediments are therefore lying just above the lower limit of the euphotic zone and may support benthic microalgae. More importantly, slightly better light and nutrient conditions may have made this site accessible to *Chara* in the past, which may have influenced sedimentation and contaminant deposition. Contaminants entering the north section of Lake St. Francis are thought to originate mainly from the Great Lakes, Cornwall (Ontario), and Massena (New York).

In contrast, station SL-26 (45°20.35′N, 73°55.78′W, depth = 15.8 m) is located in an upstream section of Lake St. Louis that has a much shorter residence time (probably less than 1 d). It is influenced by three sources of water: direct throughflow from the main channel (Lake Ontario water), outflow from the northern section of Lake St. Francis, and the Ottawa River (Fig. 1). The relative contribution of each source is unknown and probably varies with discharge. However, the low organic carbon content of the sediments of SL-26 indicates that the humic water of the Ottawa River, which drains the Precambrian Shield, has little influence on the sediment composition. The bottom sediment of this station is well below the euphotic zone and cannot support primary producers.

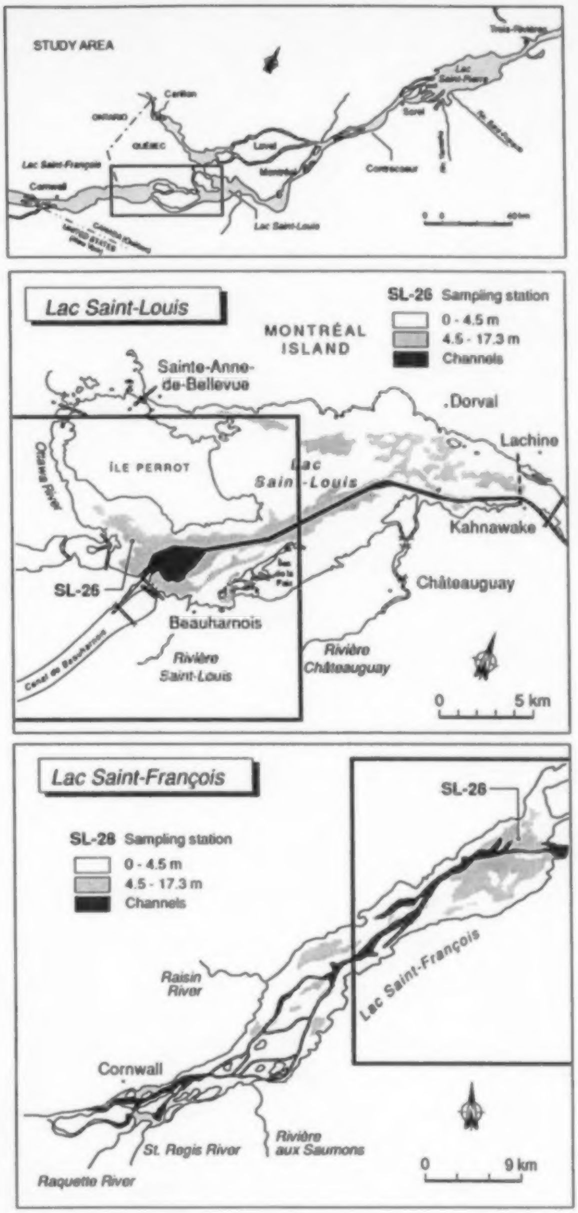
STUDY AREA
Carillon
ONTARIO
QUÉBEC
Laval
Lac Saint-Pierre
Sorel
Montréal
Contrecoeur
Lac Saint-François
Cornwall
Lac Saint-Louis
Lac Saint-Louis
SL-26 Sampling station
0 - 4.5 m
4.5 - 17.3 m
Channels
MONTRÉAL ISLAND
Sainte-Anne-de-Bellevue
Dorval
Lachine
ÎLE PERROT
Ottawa River
Lac Saint-Louis
Kahnawake
SL-26
Châteauguay
Beauharnois
Canal de Beauharnois
Rivière Saint-Louis
Rivière Châteauguay
0
5 km
Lac Saint-François
SL-28
SL-28 Sampling station
0 - 4.5 m
4.5 - 17.3 m
Channels
Lac Saint-François
Raisin River
Cornwall
St. Regis River
Rivière aux Saumons
Raquette River
0
9 km

FIG. 1. Study site showing the location of sampling stations (SL-26 (Lake St. Louis) and SL-28 (Lake St. Francis) on the St. Lawrence River, Canada.

Methods

Duplicate sediment cores were taken within 2 m of each other by divers in June of 1992. Butyrate core tubes having a 12-cm internal diameter were used. Core compaction and shortening effects were less than 3% in both cases and are ignored below. The cores were sectioned within 2 h at intervals of 1 cm (SL-26) or 2 cm (SL-28). One of the duplicate cores was used for determination of sediment texture and organic contaminants and the second core was used for all other measurements. Sediment sections reserved for organic contaminant analysis were collected in glass jars precleaned with dichloromethane and sealed with Teflon-lined caps. Sections to be analysed for total organic C (TOC), total N (TN), total P (TP), trace metals, and algal pigments were collected in polyethylene containers. All samples were immediately frozen in dry ice and kept frozen until freezer-dried. Particle size distribution was determined by X-ray sedigraphy (Duncan and Lahaie 1979; Coakley and Syvitski 1991) after sample dispersion in sodium metaphosphate.

Radioisotopes (^{137}Cs, ^{226}Ra, and ^{210}Pb) were measured by low-background, Compton-suppressed gamma spectrometry corrected for sample geometry and self-absorption (Carignan et al. 1994) using Canberra detection and counting equipment similar to that described in Appleby et al. (1986). Counting efficiencies were determined by preparing dry sediments (bulk densities of 0.5–1.6 $g \cdot cm^{-3}$) labeled with standard solutions (Amersham) of mixed nuclides (QCY.48), ^{210}Pb (RBZ.44), and ^{226}Ra (RAY.44). The samples were sealed in Al vials at least 1 mo prior to counting to allow the ingrowth of ^{222}Rn and ^{214}Pb to secular equilibrium with ^{226}Ra. Unsupported ^{210}Pb was obtained by subtracting ^{214}Pb activities from total ^{210}Pb.

Chlorophyll *a* (Chl *a*) and pheophytin *a* (Pheo *a*) were measured by reverse-phase HPLC and fluorometry (Mantoura and Llewllyn 1983) after overnight extraction of the freeze-dried sediments in a 4:1 methanol–acetone mixture. Chl *a* and Pheo *a* standards were prepared from a commercial source (Sigma C6144) verified for purity by spectrophotometry. TN and total C were measured using a Carlo-Erba model NA-1500 CNS analyser before and after overnight reaction of the samples with 0.1 N HCl to remove carbonates. We found no detectable inorganic C and observed that HCl treatment gave total C concentrations that were 3–5% higher than those of untreated samples, presumably due to the partial dissolution of the sediment matrix. Consequently, the organic C results reported below are those obtained before HCl treatment. Trace metals were measured by ICP (Cd, Cr, Cu, Zn) or AA spectrometry (Pb, with deuterium arc correction) after complete sequential digestion of the sediments and reference material (NRC Mess-1 Marine Sediment) in refluxing HNO_3, $HClO_4$, and HF in Teflon beakers. These digestion solutions were also used for TP determinations.

PCB congeners, DDT derivatives, hexachlorobenzene (HCB), and Mirex were extracted with a mixture of acetone–hexane and dichloromethane. The extracts were dried over sodium sulfate, followed by cleanup and fractionation on Florisil. Analyses were performed (Novalab Inc.) on a HP 5800 series II gas chromatograph equipped with dual capillary column/dual electron capture detectors. A HP 7673 autosampler was used to inject 1-μL splitless aliquots. Calibration and peak identification were performed using standard reference material (GLB-1, National Research Council of Canada) and individual congener standards. In addition to the highly toxic non-ortho-substituted coplanar compounds (IUPAC Nos. 77, 126, and 169), five congeners known to be mixed-function oxidase inducers (Nos. 105, 118, 128, 138, and 170) were chosen on the basis of potential toxicity. Congeners 101, 153, 180, 183, and 194 were chosen based on their frequency of occurrence in environmental samples. For PCB congeners, recoveries of standard spikes ranged between 83 and 99% with CV's of 6–9% ($n = 8$). Recoveries ± CV's were 94 ± 5% for HCB, 84 ± 10% for Mirex, 89 ± 6% for *p,p′*-DDE, and 81 ± 15% for *p,p′*-DDD. The results reported below are not corrected for recovery. Detection limits ranged from 60 $pg \cdot g^{-1}$ for PCB congeners to 100 $pg \cdot g^{-1}$ for DDT derivatives. The sum of the 13 PCB congeners reported in this study represents about 25% of the total PCB's present (B. Quémerais et al., Environment Canada, 105 McGill, Montreal, QC H2Y 2E7, personal communication).

Results and Discussion

Sediment Dating

^{210}Pb chronologies are normally based on the assumptions that either the ^{210}Pb concentration at the sediment surface (CIC model) or the rate of supply of ^{210}Pb (CRS model) has remained constant with time or that these quantities have varied in a known manner (see Oldfield and Appleby 1984). These assumptions are particularly doubtful in the fluvial lakes of the St. Lawrence. Submersed macrophytes may have been intermittently present at SL-28 and may have influenced sediment deposition. Shore and land erosion in the watershed may have varied during the last century due to changing water levels and land use. This may have diluted to a variable and unknown degree the unsupported ^{210}Pb activity of surface sediments. CRS dating can correct for variations in bulk sediment deposition (Appleby and Oldfield 1978) provided that the rate of ^{210}Pb supply has remained constant with time and that the unsupported ^{210}Pb integral (total ^{210}Pb less that supported by ^{226}Ra decay) is in secular equilibrium with the rate of unsupported ^{210}Pb supply. However, independent observations (^{137}Cs and Mirex profiles) show that sediment accumulation only began around 1940–50 at the two stations. Thus, a considerable fraction of the integral needed to calculate CRS sediment ages is missing.

Because of these methodological limitations and despite the associated potential interpretation problems, we assumed here that surface concentrations of unsupported ^{210}Pb and rate of bulk sediment deposition have remained constant with time at both sites. This approach is justified to some extent by the exceptionally constant (for fluvial environments) physical texture of the profiles (see below). Average sediment accumulation rates were thus estimated by nonlinear regression of

(1) $C_m = C_0 \exp[-(k/r)m]$

where C_0 is the unsupported ^{210}Pb concentration (becquerels per gram, from Fig. 2) at the sediment surface, C_m is the unsupported ^{210}Pb concentration at cumulative mass m (grams per square centimetre), k is the decay constant ($0.0311 \cdot yr^{-1}$) of ^{210}Pb, and r is the average sedimentation rate (grams per square centimetre per year). C_m and r were allowed to float:

Station SL-26, Lake St. Louis:

(2) $C_m = 0.179 \exp(-0.084m)$; $r^2 = 0.96$

Station SL-28, Lake St. Francis:

(3) $C_m = 0.176 \exp(-0.049m)$; $r^2 = 0.86$.

Correspondence between sediment depth and age (Fig. 3)

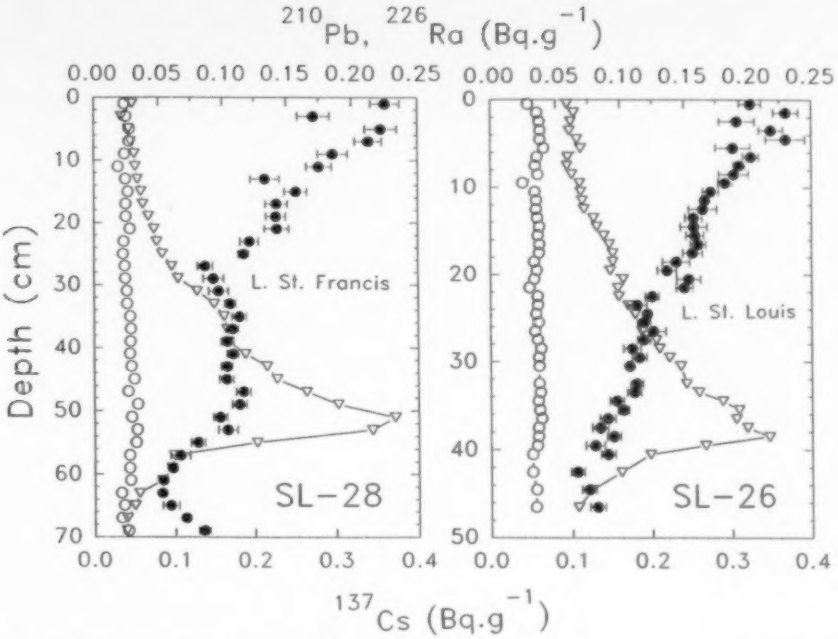

FIG. 2. Profiles of total ^{210}Pb (solid circles), ^{226}Ra (open circles, = supported ^{210}Pb), and ^{137}Cs (triangles) at stations SL-28 (Lake St. Francis) and SL-26 (Lake St. Louis). Error bars (smaller than symbols for ^{226}Ra and ^{137}Cs) represent $\pm 1\sigma$ of the net counts.

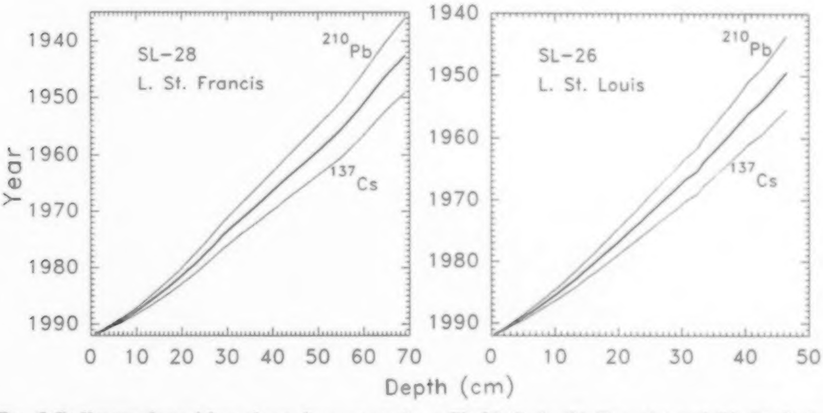

FIG. 3.Sediment deposition chronology at stations SL-28 (Lake St. Francis) and SL-26 (Lake St. Louis) averaged (thick lines) from sediment ages calculated from ^{210}Pb (upper fine lines) and ^{137}Cs (lower fine lines) sedimentation rates (see text).

was calculated by dividing the cumulative mass by *r*. Note that ^{226}Ra concentrations (and supported ^{210}Pb), which are needed to calculate unsupported ^{210}Pb, have remained constant in both cores.

An independent estimate of the average sedimentation rate was also obtained from the position of the well-defined ^{137}Cs peak, which was assumed to have been deposited in 1963. Average sedimentation rates based on ^{210}Pb (0.370 ± 0.013 and 0.635 ± 0.051 g·cm^{-2}·yr^{-1} for SL-26 and SL-28, respectively) were lower than those obtained with ^{137}Cs (0.489 and 0.829 g·cm^{-2}·yr^{-1}). The corresponding linear burial rates, averaged over the entire cores, are approximately 1.1 cm·yr^{-1} for SL-26 and 1.5 cm·yr^{-1} for Lake St. Francis. At the ^{137}Cs peak, the disagreement between both methods is 9.3 yr for SL-26 and 8.9 yr for SL-28 and reaches 10–12 yr at the bottom of the cores (Fig. 3). All dates reported below are mean dates given by both methods ± one half of the difference between them.

The poorer fit of ^{210}Pb versus cumulative mass at station SL-28 (Eq. 3) is due to the presence of anomalously high ^{210}Pb concentrations between 31 and 54 cm (Fig. 2). Interpretation of this profile based on a classical CIC model would suggest the sudden deposition of an approximately 23-cm-thick layer of homogeneous sediments around 1960–65 followed by a constant deposition of ^{210}Pb between 0 and 31 cm. This scenario appears improbable given the

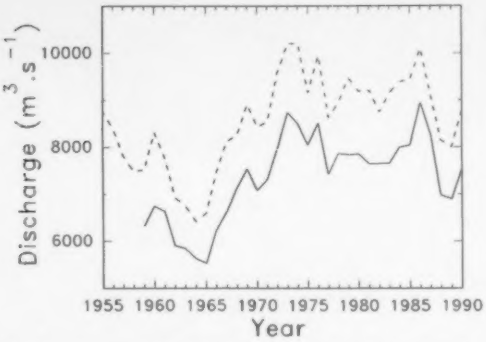

FIG. 4. Mean annual discharge at Cornwall (Lake St. Francis, solid line) and LaSalle (Lake St. Louis) for the 1955–90 interval.

constancy of sediment texture over the entire profile and given the presence of steep gradients of ^{137}Cs, trace metals, and organic contaminants within the 31- to 54-cm zone, which are inconsistent with the sudden deposition of a homogeneous sediment layer. A simpler cause can explain the ^{210}Pb anomaly at SL-28 (Lake St. Francis). According to the above-defined mean ^{210}Pb–^{137}Cs chronology, the ^{210}Pb anomaly at 31–54 cm was deposited between 1957 ± 5 and 1973 ± 2 yr. This interval corresponds to a low-discharge episode (Fig. 4) whereas the ^{210}Pb minimum at 27–28 cm is dated 1975 ± 2 yr and corresponds to a high-discharge episode which took place between 1972 and 1976. This suggests that ^{210}Pb deposition is related to discharge at this station. High ^{210}Pb concentrations between 31 and 54 cm are also associated with high C, N, and P concentrations (Fig. 5). Thus, ^{210}Pb concentrations may also be somehow influenced by, or covary with, the rate of organic matter deposition.

We tested the possible effects of annual discharge and organic matter deposition on surficial ^{210}Pb concentrations at the time of deposition by regressing decay-corrected ^{210}Pb against discharge, organic C, N, and P as independent variables for the 7- to 60-cm interval of SL-28 (n = 28) and the 5- to 47-cm interval (n = 39) of SL-26. Three sedimentation rates were used to calculate sediment ages in order to correct ^{210}Pb concentrations for decay and to attribute discharge values at the time of deposition: the average rate obtained with ^{137}Cs alone, with ^{210}Pb alone, and an average of the two previous rates (used throughout this report, except when specified). Unsupported decay-corrected ^{210}Pb concentrations (becquerels per gram) were then regressed against annual discharge (cubic metres per second), %N, %C, and %P. No significant relationships are found at SL-26. At SL-28, however, the following relationships are observed:

For ^{137}Cs dates:

$$(4)\quad {}^{210}\mathrm{Pb} = -1.2 \times 10^{-5}\ \mathrm{discharge} + 0.30\%\mathrm{N} + 0.11;\quad r^2 = 0.58$$

For ^{210}Pb dates:

$$(5)\quad {}^{210}\mathrm{Pb} = -1.5 \times 10^{-5}\ \mathrm{discharge} + 0.22\%\mathrm{N} + 0.18;\quad r^2 = 0.70$$

For average dates:

$$(6)\quad {}^{210}\mathrm{Pb} = -1.9 \times 10^{-5}\ \mathrm{discharge} + 0.19\%\mathrm{N} + 0.22;\quad r^2 = 062.$$

The effects of discharge and %N are highly significant ($p <$ 0.01) in all cases. The fact that %N is a better predictor of decay-corrected ^{210}Pb concentrations than %C suggests that the deposition of fresh organic matter influences ^{210}Pb deposition. According to the above coefficients, an increase in discharge of 3200 $m^3 \cdot s^{-1}$, such as occurred between 1965 and 1973 would decrease the rate of unsupported ^{210}Pb deposition by 20–30% at station SL-28 (Lake St. Francis).

A negative discharge effect in Lake St. Francis alone might be due to the relatively long residence time of water in its lateral sections. Lake St. Francis likely receives unsupported ^{210}Pb both from Lake Ontario and from local atmospheric fallout. Throughflow is expected to exert a strong influence on the sedimentation of local ^{210}Pb fallout when the water residence time is comparable with the settling time of ^{210}Pb in the water column. We have previously estimated the annual mean residence time of water in the lateral sections of Lake St. Francis at about 12 d (Carignan et al. 1994). Water residence time should be longer during low-discharge periods. Durham and Joshi (1980) reported an apparent settling velocity of 0.7 $m \cdot d^{-1}$ for ^{210}Pb in the surface waters of Lake Huron. Since the mean depth is 5.1 m in this lateral section of the lake, the settling time of ^{210}Pb should be about 7 d. Thus, a flow effect is likely in Lake St. Francis and should be less pronounced at station SL-26 in Lake St. Louis, where the water residence time is probably less than 1 d. In addition, low-discharge periods were probably associated with lower water levels, lower suspended matter concentrations, and, possibly, the colonization of the bottom by *Chara* at SL-28. The intermittent presence of a submersed macrophyte cover may have modified local ^{210}Pb deposition.

Three independent time markers confirm that our chronology is reasonably accurate over the entire profiles. The appearance of Mirex, a fire retardant and insecticide that began to be produced in 1960 in the Great Lakes watershed (Kaiser 1978), is dated 1960 ± 4 yr at station SL-28 and 1958 ± 5 yr at station SL-26 (Fig. 5 and 6). PCB sales rose sharply in the United States between 1956 and 1970 and declined abruptly after 1970 (Oliver et al. 1989); this event is dated 1970 ± 3 yr in Lake St. Francis and 1968 ± 4 yr in Lake St. Louis. Finally, the oldest fine-grained sediments of SL-28 rest on a sandy horizon (Fig. 5 and 6) whereas those of station SL-26 rest on a bed of large 10- to 20-cm cobbles that lined the riverbed prior to flow diversion through the Beauharnois Canal. The age of the oldest sediments at SL-28 (1943 ± 6 yr) coincides (within dating error) with the completion of the diversion of the St. Lawrence through the Beauharnois Canal in 1941. Although the oldest sediments at SL-26 are dated 1950 ± 6 yr, divers observed that deeper, and presumably older, sediments were present in voids between the cobbles.

Algal Pigments

Pigment profiles at both stations (Fig. 5 and 6) show two main features: rapidly decreasing concentrations of Chl *a* and Pheo *a* in the most recent sediments and a secondary maximum corresponding to sediments deposited between 1955 and 1970. In the upper 10 cm, pigment profiles are essentially similar to those described by Sun et al. (1991) in Long Island Sound. They can be explained by the combined effect of burial, sediment mixing, and degradation of Chl *a*. In the fluvial lakes of the St. Lawrence, the average sum-

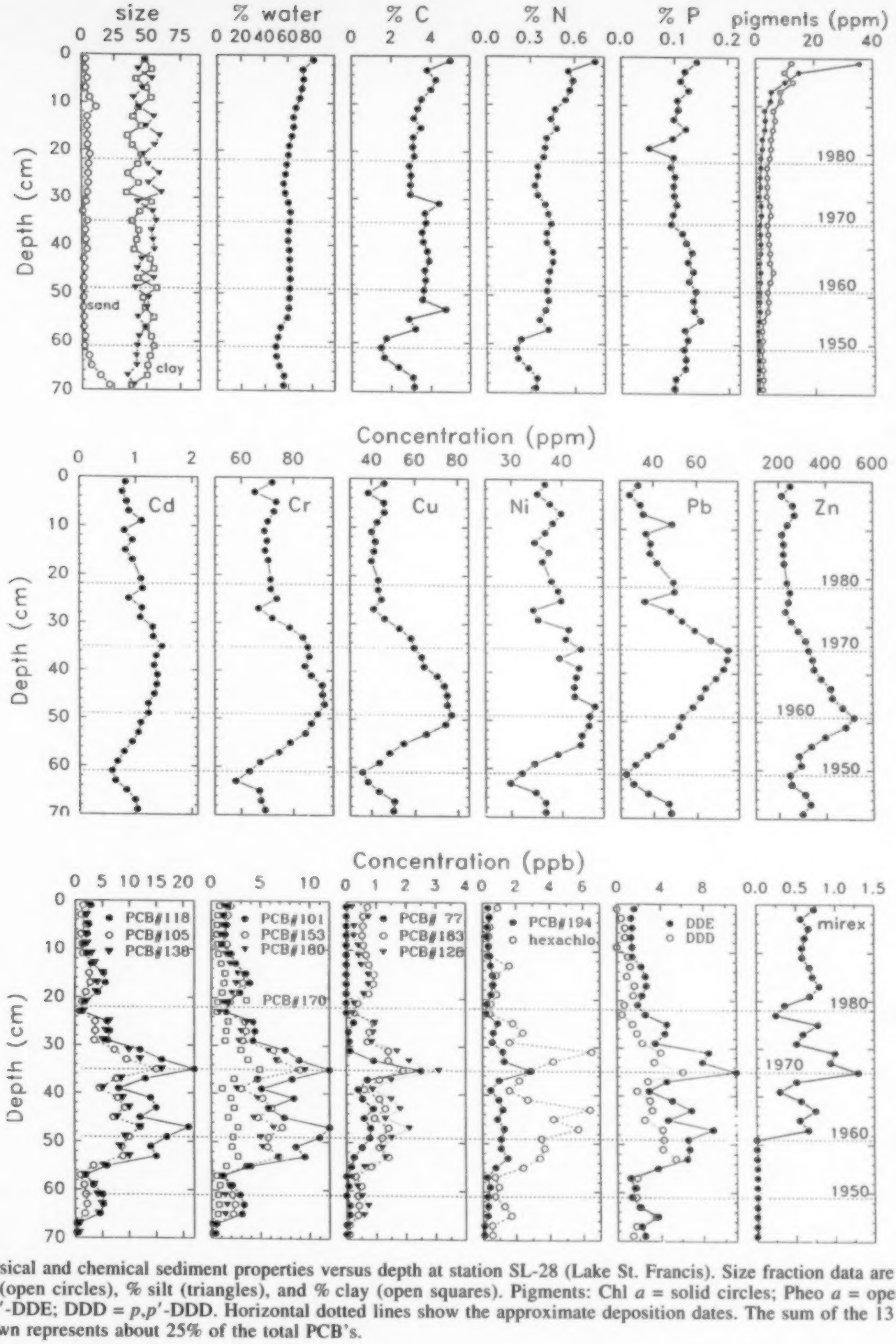

FIG. 5. Physical and chemical sediment properties versus depth at station SL-28 (Lake St. Francis). Size fraction data are expressed as % sand (open circles), % silt (triangles), and % clay (open squares). Pigments: Chl *a* = solid circles; Pheo *a* = open circles. DDE = *p,p'*-DDE; DDD = *p,p'*-DDD. Horizontal dotted lines show the approximate deposition dates. The sum of the 13 PCB congeners shown represents about 25% of the total PCB's.

mertime mixing coefficient (K_s) of superficial (0–4 cm) sediments calculated from ^{7}Be profiles is 15 cm^2·y^{-1} but span about 1 order of magnitude between sites (Carignan et al. 1994). Using the average mixing coefficient and recent (last 10 yr) sedimentation rates at stations SL-26 (1.6 cm·yr^{-1}) and SL-28 (2.4 cm·yr^{-1}), the first-order decay coefficient of

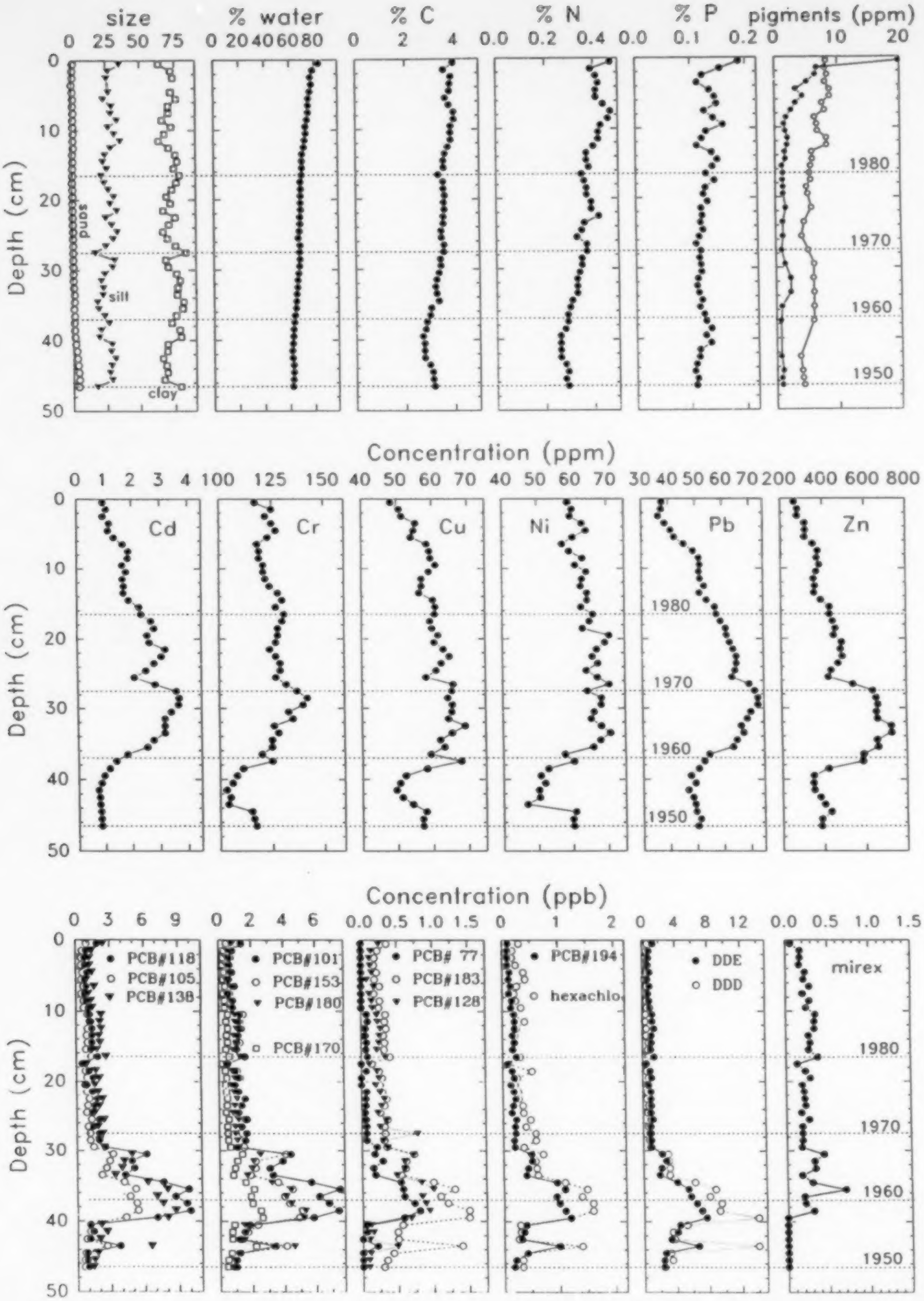

FIG. 6. Physical and chemical sediment properties versus depth at station SL-26 (Lake St. Louis). See Fig. 5 for details.

Chl *a* can be estimated with an advection–diffusion model (Van Sickle et al. 1983):

$$(7)\quad p_z C_z = p_0 C_0 \exp\left[\left(\frac{\bar{v} - (\bar{v}^2 + 4K_s k)^{1/2}}{2K_s}\right) z\right]$$

where z is depth (centimetres), p_0 and p_z are the concentrations of sediment solids (grams per cubic centimetre) at the surface and depth z, C_0 and C_z are Chl *a* concentrations at the sediment surface and at depth z, $\bar{v}$ is the average sediment burial rate (centimetre per year) within the mixed layer, and k is the decay constant of Chl *a*. Best-fitting values for k, as found by nonlinear regression of p_zC_z/p_0C_0 versus depth, are 1.4 and 0.8·yr^{-1} at SL-26 and SL-28, respectively. These values are about an order of magnitude lower than those reported by Sun et al. (1991) for coastal marine sediments but have an uncertainty of about an order of magnitude due to the uncertainty of K_s. The shape of the Pheo *a* profiles in the upper 20 cm of both cores is also suggestive of decomposition, but at a slower rate than for Chl *a*. The factors controlling the rate and extent of algal pigment degradation in sediments are virtually unknown but may involve invertebrate activity and the availability of electron acceptors (O_2, NO_3^-, SO_4^{2-}) which become depleted within the upper 3 cm at these stations (M.A. Huerta-Diaz and R. Carignan, unpublished data). Nevertheless, as observed by Sun et al. (1991) and by all paleoecologists using fossil pigments to infer past productivity, a small residual proportion of Chl *a* escapes degradation and gets permanently buried.

At station SL-26, this residual Chl *a* shows a clear secondary maximum between 1961 ± 4 and 1969 ± 3 yr, where it increased by a factor of about 2 during the mid-1960's. Pheo *a* shows a slightly broader maximum between 1959 ± 4 and 1972 ± 3 yr. At station SL-28, there is a detectable twofold increase in Pheo *a* between 1956 ± 5 and 1972 ± 3 yr but no corresponding secondary Chl *a* maximum. These data suggest that algal deposition (planktonic or periphytic) was higher during the 1960's than before the mid-1950's and after 1975. Direct monitoring of Chl *a* in offshore Lake Ontario since 1968 confirms that summertime Chl *a* concentrations have been decreasing steadily by a factor of 2, from a maximum of 4.6 μg·L^{-1} reached in 1973–76 to 2.2 μg·L^{-1} in 1990 (H. Dobson, National Water Research Institute, 867 Lakeshore Road, Burlington, ON L7R 4A6, personal communication). Thus, fossil pigments appear to have some value as indicators of past productivity in the St. Lawrence, but their preservation seems to be variable between stations, and diagenetic effects prohibit their use in the most recent sediments.

Carbon and Nutrients

It is estimated that P loading to Lake Erie increased by a factor of 5 (4000–20 000 t·yr^{-1}) between 1940 and 1966 (Burns and Ross 1972). Chapra (1977) calculated an increase from 3000 t·yr^{-1} in the 1800's to 16 000 t·yr^{-1} in the 1970's for Lake Ontario. For the same lake, Stevens and Neilson (1987) reported a decrease from 14 600 t·yr^{-1} in 1969 to 8900 t·yr^{-1} in 1982. It is also known that TP concentrations in the offshore waters of Lake Ontario decreased by 60%, from 25 μg·L^{-1} in 1970 to 10 μg·L^{-1}, in 1990 due to a phase-out of phosphate detergents and to improved waste water treatment (Stevens and Neilson 1987; H. Dobson, NWRI, personal communication). Interestingly, this nutrient pulse left no clear P, N, or organic C signal in the sediments of Lake St. Louis (SL-26), except for a small P increase around 1956. Decreasing C, N, and P concentrations within the first 20 cm at this station are most probably diagenetic and may have masked historical anthropogenic influences.

In contrast, the concentrations of pigments, C, N, and P are higher in the superficial sediments of SL-28 than at SL-26, and clear nutrient signals have been left between 1955 and 1975. These differences may reflect again the different environments of both stations. Indeed, favorable conditions for an efficient use of nutrients by phytoplankton, submersed macrophytes, and epiphytes prevail in the water mass influencing station SL-28 due to its relatively long residence time, shallow mean depth, and high water transparency. Furthermore, the molar C:N ratio of 10 for the increase in C and N between 1955 and 1974 is indicative of fresh organic matter. At station SL-26, turbulence and poor light conditions in the main channel of the St. Lawrence and Ottawa rivers are less favorable to algal and macrophyte growth.

Trace Metals

Preindustrial trace metal concentrations in the St. Lawrence sediments must first be established in order to evaluate the extent of past and present anthropogenic contamination. Very old (approximately 8000 yr) undisturbed fine-grained glaciolacustrine deposits are common in the river bed of the St. Lawrence. These sediments are unsuitable to estimate preindustrial trace metal concentrations, since they contain virtually no organic matter compared with the recent sediments of the St. Lawrence, which usually contain 0.5–5% of organic C. Thus, preindustrial concentrations of metals having an affinity for organic matter would be underestimated if glaciolacustrine deposits were used. However, four cores described in Carignan et al. (1994) can be used to estimate preindustrial levels. In their lowermost part, these cores have organic C concentrations that are typical of modern surface deposits, but have undetectable unsupported ^{210}Pb, which means that their oldest sediments must be older than about 130 yr. One of these cores (SL-16), obtained in Lake St. Louis, has clay-sized (approximately 40%) and silt (approximately 60%) fractions comparable with those observed at SL-26 and SL-28 and 1.1% of organic C. Average trace metal concentrations in the lowermost 35- to 45-cm segment of SL-16 are 0.15 ppm Cd, 62 ppm Cr, 17 ppm Cu, 32 ppm Ni, 15 ppm Pb, and 78 ppm Zn. Most of these values are comparable with the average elemental abundances in shale compiled by Krauskopf (1967), e.g., 0.2 ppm Cd, 100 ppm Cr, 57 ppm Cu, 95 ppm Ni, 20 ppm Pb, and 80 ppm Zn. Trace metal concentrations observed in the old sediments of SL-16 thus appear to be representative of uncontaminated preindustrial sediments in the St. Lawrence. They are used here as a reference against which to compare anthropogenic influences.

Cores taken at SL-26 and SL-28 show highly significant reductions in trace metal concentrations since 1960 (Table1), but slightly different pollution chronologies (Fig. 5 and 6). In Lake St. Francis (SL-28), at the beginning of the sedimentary record (1943 ± 7 yr), all trace metal concentrations already exceeded levels expected for unpolluted preindustrial sediments and increased rapidly between 1950 ± 6 and 1960 ± 4 yr. Cr, Cu, Ni, and Zn concentrations reached their maximum values in 1960 ± 4 yr and decreased markedly during the following 20 yr. Cd and Pb concentrations reached their maximum values only in 1970 ± 3 yr. During the last 10 yr, metal concentrations have not significantly ($p > 0.05$) decreased, except for Pb (Table 2).

In Lake St. Louis (SL-26), trace metal concentrations increased rapidly between 1955 ± 5 and 1965 ± 4 yr. Cu and Zn show a broad maximum between 1960 ± 4 and 1970 ± 3 yr. Ni reached a maximum in 1963 ± 4 yr and has been monotonically decreasing ever since. Cd, Cr, and Pb have a well-defined maximum near 1969 ± 3 yr. In contrast with Lake St. Francis, all trace metals have continued decreasing

TABLE 1. Simple or multiple linear regression models for metal concentrations (ppm) versus sediment age (yr) and mean annual discharge ($m^3 \cdot s^{-1}$) for the 1960–90 interval. *Significant at the $p < 0.05$ level; **significant at the $p < 0.01$ level; ns: no significant relationship found at the $p < 0.05$ level. For this interval, metal concentrations were not significantly related to clay content.

Station	Metal		Age		Discharge		Constant	r^2
SL-26	Cd	=	0.069**		ns	+	1.5	0.54
	Cr	=	0.36**		ns	+	123	0.31
	Cu	=	0.33**		ns	+	56	0.67
	Ni	=	0.26**		ns	+	62	0.50
	Pb	=	1.12**	+	0.0030**	+	18.3	0.87
	Zn	=	12.7**	−	0.022**	+	510	0.91
SL-28	Cd	=	0.014**		ns	+	0.93	0.46
	Cr	=	0.64**	−	0.0023*	+	86	0.82
	Cu	=	1.03**	−	0.0042**	+	71	0.88
	Ni	=	0.22**	−	0.0012*	+	46	0.71
	Pb	=	0.83**		ns	+	46	0.42
	Zn	=	6.75**	−	0.0336**	+	462	0.87

TABLE 2. Simple or multiple linear regression models for metal concentrations (ppm) versus sediment age (yr), mean annual discharge ($m^3 \cdot s^{-1}$), and clay content (%) for the 1980–90 interval. *Significant at the $p < 0.05$ level; **significant at the $p < 0.01$ level; ns: no significant relationship found at the $p < 0.05$ level.

Station	Metal		Age		Discharge		Clay		Constant	r^2
SL-26	Cd	=	0.09**		ns		ns	+	1.31	0.70
	Cr	=	0.54*		ns	+	0.62**	+	77.0	0.67
	Cu	=	ns	+	0.00219*		ns	+	38.6	0.37
	Ni	=	0.39*		ns		ns	+	60.7	0.28
	Pb	=	1.47**	+	0.0023*		ns	+	22.1	0.91
	Zn	=	9.94**		ns		ns	+	322	0.71
SL-28	Cd	=	ns		ns		ns		—	—
	Cr	=	ns		ns		ns		—	—
	Cu	=	ns		ns		ns		—	—
	Ni	=	ns	−	0.0020**		ns	+	53.4	0.67
	Pb	=	1.72**		ns	+	0.65*	+	5.1	0.65
	Zn	=	ns	−	0.021*		ns	+	398	0.49

at a more or less constant rate between 1970 and 1990 and show significant reductions during the last decade (Table 2). Concentrations in surficial sediments are close to those observed at SL-28.

Excess trace metal concentrations due to human activity are often expressed as an anthropogenic enrichment factor (AEF = (anthropogenic + natural) / natural). In the most recent (1992) sediments of SL-28, AEF values are 1.1 for Cr, 1.2 for Ni, 2.2 for Pb, 2.6 for Cu, 3.1 for Zn, and 5.4 for Cd. At SL-26, recent AEF values are slightly higher: 2.0 for Cr, 1.9 for Ni, 2.5 for Pb, 2.9 for Cu, 3.5 for Zn, and 6.7 for Cd. Thus, some AEF's (Cr, Ni) are now approaching unity whereas they are still quite high in some other cases (Zn, Cd). It should be noted that enrichment factors derived from total metal concentrations are likely to be lower than those derived from concentrations of the reactive metal fractions and may give an overly optimistic image of current contamination levels.

In both cores, Cd and Pb peaks are synchronous and occurred near 1970. Maximum Pb concentrations coincide, within dating error, with peak use of leaded gasoline between 1969 and 1974 in North America (Trefry et al. 1985). The date (1969–70) of the Pb maximum observed in the St. Lawrence coincides exactly with that found by Trefry et al. (1985) in the Mississippi Delta. This observation supports the accuracy of our chronology and suggests that the anthropogenic Pb peak is a reliable pangeographic chronological marker in North America.

The highly significant decreases in metal concentrations after 1960 in both cores are very likely due to historical loading reductions to the river. However, other factors independent of anthropogenic metal loading may have contributed to modulate the evolution of metal concentrations. These factors include variations in river discharge, which are expected to influence the degree of dilution of local industrial/urban metal inputs, sediment particle size, and organic matter content, as found above for ^{210}Pb. The possible importance of these factors can be examined using multiple regression with sediment age (as a surrogate for past loading), river discharge, and clay content as independent variables. The results suggest that during the 1960–90 interval, discharge has influenced metal concentrations, while clay content had no significant effect (Table 1). Although trace metals are usually preferentially associated

TABLE 3. Simple or multiple linear regression models for metal concentrations (ppm) versus sediment age (yr), mean annual discharge ($m^3 \cdot s^{-1}$), clay content (%), organic C (%), and TN (%) for the 1962–82 interval. *Significant at the $p < 0.05$ level; **significant at the $p < 0.01$ level; ns: no significant relationship found at the $p < 0.05$ level. For this interval, the clay content had no significant ($p > 0.05$) effect on metal concentrations.

Station	Metal	Age	Discharge	TN	Constant	r^2
SL-26	Cd	= 0.082**	ns	+ 10.9**	− 2.50	0.53
	Cr	= ns	ns	ns	—	—
	Cu	= 0.34**	− 0.0011*	+ 68**	+ 42	0.67
	Ni	= 0.18*	ns	ns	+ 64	0.20
	Pb	= 1.08**	+ 0.0016*	+ 71*	+ 6.1	0.77
	Zn	= 12.8**	− 0.028*	ns	+ 559	0.85
SL-28	Cd	= ns	ns	+ 3.34**	− 0.09	0.69
	Cr	= 0.75**	ns	+ 102**	+ 26.7	0.95
	Cu	= 1.43**	− 0.0016*	+ 82.5**	+ 11.3	0.90
	Ni	= 0.40**	ns	ns	+ 33.7	0.59
	Pb	= ns	+ 0.008*	+ 217**	− 28.0	0.54
	Zn	= 13.2**	ns	ns	+ 93	0.93

with the smallest size fractions, chronological variations in the clay-sized fraction were probably too small at both sites to have a detectable influence on metal concentrations. In Lake St. Louis (SL-26), significant flow effects are detected for Pb (positive) and Zn (negative). In Lake St. Francis (station SL-28), significant negative flow effects are detected for Cr, Cu, Ni, and Zn. When the same analysis is repeated for the recent past (1980–90), the effect of discharge is significant (positive) for Pb only in core SL-26 and significant (negative) for Ni and Zn in core SL-28. The relatively long residence time of Lake St. Francis may explain, again, why the effect of discharge is more pronounced in this lake.

The C and N profiles suggest that considerable organic matter diagenesis occurs during the first 10 yr or so following sediment burial. This period must therefore be excluded in the search for a possible influence of organic matter deposition on trace metal concentrations. Multiple regressions of trace metal concentrations versus sediment age, river discharge, %clay, %C, and %N performed for the 1962–82 period (Table 3) indicate that organic matter concentrations are positively related to Cd, Cu, and Pb concentrations in core SL-26 and to Cd, Cr, Cu, and Pb concentrations in core SL-28. In these regressions, %N generally had a slightly better explanatory success than organic C. Clay content had no significant effect. Thus, historic trends in metal concentrations and deposition appear to have been influenced not only by changing anthropogenic inputs and discharge, but also by fresh organic matter deposition. The positive effect of organic matter on trace metal concentrations in sediments could be attributable to trace metal scavenging and deposition by algae (Sigg et al. 1987) and provides support for the existence of significant interactions between organic matter and trace metal dynamics in the St. Lawrence.

The values of the regression constants for discharge and %N indicate that their influence on metal concentrations might be considerable. For example, the constant describing the effect of discharge on Zn (Table 1) suggests that Zn concentrations decrease by 21 ppm (Lake St. Francis) and 34 ppm (Lake St. Louis) for each 1000 $m^3 \cdot s^{-1}$ increment in annual discharge. Between 1960 and 1975, discharge changed by as much as 3800 $m^3 \cdot s^{-1}$, which means that changes in Zn concentrations of the order of 80 and 130 ppm for Lakes St. Francis and St. Louis could be due to variations in discharge only. Thus, the low-discharge period that occurred in 1988–89 (Fig. 4) may be responsible for the subsurface peaks of Cd, Cr, Cu, Ni, and Zn present near 6 cm at station SL-28 and those of Cr, Cu, and Ni present near 4.5 cm at station SL-26. In this latter case, the 25% reduction in discharge that occurred in 1989–90 caused a 20–30% increase in most metals. Thus, discharge seems to have an inversely proportional effect on sediment metal concentrations. Similarly, regression parameters describing the relationship between TN (below the diagenetically active layer) and metal concentrations indicate that a change in N content of 0.2%, such as observed between 20 and 60 cm in core SL-28, could be responsible for variations of 18 ppm for Cu, 18 ppm for Cr, and 47 ppm for Pb.

While the effect of discharge is negative for Cr, Cu, Ni, Zn, and ^{210}Pb, it is positive for Pb (Tables 1–3). This may reflect different relative importances of local and external sources for each metal. If pollutants were released into the St. Lawrence mainly via local industrial and urban effluents, discharge from Lake Ontario should have a negative (diluting) effect. If, on the other hand, Lake Ontario was the main source, pollutant loading to the fluvial lakes may increase with river discharge. Nriagu and Pacyna (1988) have estimated the atmospheric contribution of metal inputs to aquatic ecosystems to be 6, 9, 9, 72, and 18% for Cr, Cu, Ni, Pb, and Zn, respectively. Thus, Pb loading to the St. Lawrence is expected to have a large atmospheric component compared with other metals, and a large fraction of the Pb load may originate from Lake Ontario. The positive discharge effect observed for Pb is hard to reconcile with the opposite effect noted for ^{210}Pb (Eq. 4–6), which also has a predominantly atmospheric origin. This apparent inconsistency may be due to differences in their geochemical behavior (chemical form, biological availability, settling velocity).

Organic Contaminants

The organic contaminant profiles (Fig. 5 and 6) display noticeable features: past and recent concentrations are about

20 times lower than observed in Lake Ontario sediments (Oliver et al. 1989). Concentrations declined by a factor of 5–10 between the mid-1960's and the early 1980's at both stations, except Mirex, which shows no obvious trend with time. At a given station, most contaminant profiles are strikingly similar although their history of utilization has been different. Lastly, there are marked differences in the shape of the profiles between the two stations.

At the beginning of the sedimentary record at station SL-28 (1943 ± 6 yr), Mirex concentrations are undetectable and PCB congeners are either undetectable or present at very low (<1 ppb) concentrations whereas significant concentrations of HCB and DDT derivatives are already present. The presence or absence of particular contaminants in the oldest sediments is consistent with their respective production history, which began in the mid-1920's for HCB, between 1930 and 1940 for most PCB congeners, in the early 1940's for DDT, and in 1960 for Mirex. At both stations, all contaminants, except Mirex, show a small, and probably synchronous, early peak dated 1949 ± 6 yr in Lake St. Francis and 1953 ± 5 yr in Lake St. Louis. The cause of this early peak is unknown. Subsequently, most contaminants increased markedly during the late 1950's and reached a second, more pronounced maximum around 1958–63. Concentrations then decreased significantly during the mid-1960's and reached a third maximum near 1970 ± 3 yr. This third maximum is more pronounced at SL-28 than at SL-26. The peculiar multipeak shape of the profiles is not related in any obvious way to their production or use history reported in Oliver et al. (1989), except that the period of maximum contaminant concentrations in the sediments (1960–70) coincides, within dating error, to the period of maximum production or use of these substances in the United States. The multipeak profiles of the St. Lawrence are quite different from those observed in Lake Ontario, where single broad contaminant concentration maxima centered around 1965 are usually present (Durham and Oliver 1983; Oliver et al. 1989).

The absence of a strong Mirex concentration peak during the 1960's at both stations and the absence of declining concentration trends during the last 20 yr are particularly interesting. Clear peaks corresponding to the period of maximum production of this contaminant have been observed in Lake Ontario sediments, near the mouth of the Niagara River (Durham and Oliver 1983), and at three deep stations (Oliver et al. 1989). Since Mirex found in the St. Lawrence originates essentially from Lake Ontario, its profiles suggest that the contamination signal received from Lake Ontario is considerably dampened (several decades), possibly as a combined effect of the long (7 yr) water residence time in Lake Ontario and the slow burial rate of contaminated sediments in most of its basin. Because no obvious trend with time is apparent in the St. Lawrence sediments, Mirex loading from Lake Ontario to the St. Lawrence is likely to remain near current values for at least several decades. Mirex is probably a good tracer for other hydrophobic organic chemicals derived from Lake Ontario which have similar octanol/water partition coefficients. If this is the case, then other hydrophobic chemicals originating from Lake Ontario should have left equally dampened signals in the St. Lawrence sediments. Since all other hydrophobic contaminants reported in this study show large peaks between 1950 and 1970, it is tempting to conclude that their origin has had an important local component (direct inputs of urban, agricultural, and industrial effluents between Kingston and Montréal).

Between 1970 and 1980, contamination trends have differed somewhat at both stations. At SL-28, concentrations reached an absolute maximum in 1970 ± 3 yr and gradually decreased until 1980. At SL-26, concentrations reached a secondary maximum in 1967 ± 4 yr and suddenly decreased to current levels in less than 2 yr. In general, concentration changes have been more abrupt at SL-26 than at SL-28. For example, the earliest contaminant peak, dated 1953 ± 5 yr at SL-26, lasted less than 2 yr whereas its counterpart at SL-28, dated 1949 ± 6 yr, lasted for at least 5 yr. The dampening of the peaks at SL-28 supports earlier results (Carignan et al. 1994) indicating that the residence time of the mobile sediments is much longer in Lake St. Francis (up to 8 yr) than in Lake St. Louis (2 yr). Thus, the comparatively slow decrease of contamination levels between 1970 and 1980 in Lake St. Francis may not be due to different contamination histories in the two lakes. Rather, the larger mass of contaminated sediments present in Lake St. Francis may have taken more time to respond to a decrease in contaminant loading.

During the entire record, organic contaminant concentrations have remained higher at SL-28 than at SL-26 by a factor of about 2. This difference is not due, as might have been expected, to a higher organic C and/or clay-sized fraction concentrations at SL-28; in fact, the sediments of SL-28 are coarser and have organic C concentrations that are comparable with those of SL-26. Note also that although organic contaminant concentrations are higher at SL-28 than at SL-26, the opposite is true for most trace metals except Pb which shows similar concentrations at both stations and Cu which reached slightly higher concentrations at SL-28 around 1960. This indicates that the two stations have been influenced by different contaminant sources or that the biological or physical factors promoting contaminant deposition have been different at the two sites.

The upper part of the sedimentary record (1980–92) shows a substantial decrease in contaminant levels compared with those observed during the 1960's, except Mirex, which has remained more or less constant. However, even if the use of DDT and production of Mirex had completely ceased by 1971 and 1976, considerable variations in concentrations still occurred during the 1980's. In Lake St. Francis, for example, concentrations reached an absolute minimum in 1979 ± 2 yr but subsequently increased by a factor of 2–5 in 1983–86. The same behavior is observed for PCB's and HCB, except for congener 77, which became undetectable after 1980. Similar, but less pronounced trends also exist in Lake St. Louis.

The observation that the concentrations of unrelated organic contaminant families have varied in a similar way with time, that several peaks unrelated to contaminant use or production history are present, and that levels have kept fluctuating after phase-out strongly suggest that one or more factors independent from use of or production of these substances have influenced contamination levels in the St. Lawrence. As proposed above for trace metals, river discharge is a likely candidate. We have explored this hypothesis by regressing organic contaminant concentrations against river discharge at the time of deposition and contaminant production, use, or sales in the United States for two periods: the 1960–72

TABLE 4. Simple or multiple linear regression models for organic contaminant concentrations (ppb) versus discharge ($m^3 \cdot s^{-1}$) and contaminant source expressed as production (P) or sales (S) 10^3 $t \cdot y^{-1}$) in the United States. *Significant at the $p < 0.05$ level; **significant at the $p < 0.01$ level; ns: no significant relationship found at the $p < 0.05$ level.

Station	Interval	Contaminant		Discharge		Source	Constant	r^2
SL-26	1963–72	PCB 101	=	-1.1×10^{-3}**		ns	+ 11	0.80
	1963–72	PCB 105	=	-1.4×10^{-3}**		ns	+ 14	0.81
	1963–72	PCB 118	=	-1.9×10^{-3}**		ns	+ 19	0.76
	1963–72	PCB 153	=	-2.6×10^{-3}**		ns	+ 26	0.82
	1960–70	DDE	=	-1.9×10^{-3}**	+	$4.7 \times 10^{-2}P$**	+ 16	0.89
	1960–70	DDD	=	-3.1×10^{-3}**	+	$5.9 \times 10^{-2}P$**	+ 26	0.86
	1961–72	Mirex	=	8.8×10^{-5}*	+	$1.2 \times 10^{-3}S$**	− 0.5	0.58
SL-28	1961–72	Mirex	=	3.9×10^{-4}**	+	$3.4 \times 10^{-4}S$**	− 2.5	0.76

TABLE 5. Linear regression models for organic contaminant concentrations (ppb) versus discharge (Q, $m^3 \cdot s^{-1}$) in Lake St. Francis (station SL-28) for the 1980–90 interval.

Contaminant		Model			r^2
SL-26					
Mirex	=	$6.50 \times 10^{-5}Q$*	−	0.31	0.45
SL-28					
PCB 101	=	$1.15 \times 10^{-3}Q$*	−	6.6	0.43
PCB 118	=	$1.84 \times 10^{-3}Q$*	−	11.2	0.38
PCB 153	=	$0.97 \times 10^{-3}Q$*	−	5.3	0.50
PCB 105	=	$0.92 \times 10^{-3}Q$*	−	5.3	0.42
PCB 138	=	$1.36 \times 10^{-3}Q$*	−	7.4	0.40
PCB 180	=	$0.79 \times 10^{-3}Q$*	−	4.4	0.40
PCB 170	=	$0.40 \times 10^{-3}Q$*	−	2.2	0.46
HCB	=	$0.38 \times 10^{-3}Q$*	−	2.3	0.35
DDE	=	$0.70 \times 10^{-3}Q$**	−	3.3	0.56

period, when production and use of these contaminants were high, and the recent 1980–90 period, when production and use had been strongly reduced or abandoned.

During the high-contamination period (1966–70), river discharge and contaminant production and/or use fluctuated considerably from year to year. Consequently, small dating errors could easily obscure possible relationships, or even produce spurious results. Since the uncertainty of the average ^{210}Pb–^{137}Cs dates is rather large (3–4 yr) for this interval, we recalculated a deposition chronology between 1960 and 1972 based on the position of the two most reliable time markers available within this interval: the ^{137}Cs peak, which we assumed to correspond exactly to 1963, and the sudden decline of domestic sales of PCB in 1970 (Peakall 1975), which we assumed to correspond to the 30- to 32-cm section of SL-28 and to the 29- to 30-cm section of SL-26 (Fig. 5 and 6). Concentrations of Mirex, DDT derivatives and selected PCB congeners were then regressed against discharge, production, or sales data taken from the U.S. Tariff Commission (1973), Peakall (1975), and Kaiser (1978). The results (Table 4) suggest that during the 1960–72 interval, Mirex concentrations in the sediments of both stations were positively related to river discharge and Mirex sales in the United States. However, DDT derivatives (1960–70) were negatively related to discharge and positively related to production (but not to use) at station SL-26 only. PCB concentrations (1963–72) were negatively related to discharge at station SL-26 only. At station SL-28, no significant relationships were found between DDT derivatives or PCB's and discharge or production.

These results should be interpreted with caution, since even small dating errors could obscure existing relationships between contaminants and discharge. Furthermore, it is also possible that contaminant loading to the St. Lawrence happened to be high during periods of low discharge with no causal relationship between the two phenomena. Nevertheless, the positive discharge effect for Mirex at both stations is consistent with the fact that Lake Ontario is the only known source for this contaminant; therefore, Mirex loading to the St. Lawrence should have been proportional to discharge from Lake Ontario. The negative discharge effect on DDT derivatives and PCB's suggests that sources were mainly local at station SL-26 during the 1960–70 decade and that high-discharge events had a diluting effect, as proposed above for some trace metals. The apparent absence of a discharge effect for PCB's and DDT derivatives at SL-28 may be due to small dating errors or to an equivalent importance of local and external sources at this station.

For the 1980–90 interval, the ^{210}Pb–^{137}Cs dates are more reliable (±1 yr) and were used to calculate discharge at the time of deposition. Only discharge was used as an independent variable. The results (Table 5) suggest that for PCB's, DDT derivatives, and HCB, recent contamination levels have been directly proportional to discharge at station SL-28 whereas a discharge effect is only seen for Mirex at SL-26. Thus, it would seem that Lake Ontario is now the major contaminant source for Lake St. Francis whereas local and external sources share a similar importance in Lake St. Louis.

Conclusion

Two cores taken in the fluvial lakes of the St. Lawrence show that biological productivity and contamination by trace metals and organic chemicals were much higher in the 1960's and 1970's than they are now. Inferred chronological changes in algal pigments and nutrients generally correspond to eutrophication trends directly measured in Lake Ontario. Concentrations of trace metals and organic contaminants are much less susceptible to postdepositional diagenetic alterations than are the concentrations of algal pigments and nutrients. The inferred metal and organic pollution chronologies are likely more accurate than the eutrophication chronology deduced from algal pigments and nutrients.

Anthropogenic trace metal enrichment factors are now approaching unity in some cases (Cr, Ni, Pb). It should be noted, however, that these factors are derived from total metal concentrations and not from the toxicologically more relevant reactive fractions. Our data provide some indications that river discharge influences year-to-year variations in contamination levels in the St. Lawrence and that the importance of local versus upstream sources has varied with time. These hypotheses should be taken into consideration in future trend analyses of current monitoring data.

Acknowledgements

We thank Sylvie St-Pierre for technical assistance and the National Water Research Institute of Environment Canada for performing the particle-size analyses. Financial and logistic support was provided by the Centre Saint-Laurent, Environment Canada.

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Mitochondrial DNA Diversity in Jackass Morwong (*Nemadactylus macropterus*: Teleostei) from Australian and New Zealand Waters

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Grewe, P.M., A.J. Smolenski, and R.D. Ward. 1994. Mitochondrial DNA diversity in jackass morwong (*Nemadactylus macropterus*: Teleostei) from Australian and New Zealand waters. Can. J. Fish. Aquat. Sci. 51: 1101–1109.

The jackass morwong (*Nemadactylus macropterus*), a commercially valuable marine fish in the Australian – New Zealand region, was surveyed for genetic variation as part of a larger project aimed at clarifying its stock structure. Mitochondrial DNA variation in 166 jackass morwong from seven southern Australian localities was examined using nine restriction enzymes. The 28 haplotypes identified gave an overall nucleon diversity of 0.671. Mean nucleotide diversity per sample was 0.458%, with a (corrected) nucleotide divergence among samples of 0.001%. There was no significant spatial patterning. Five hundred individuals from eight southern Australian localities and one New Zealand locality were examined using three restriction enzymes detecting polymorphic cut sites. The 33 haplotypes identified gave an overall nucleon diversity of 0.635. Mean nucleotide diversity per sample was 1.247%, with a (corrected) nucleotide divergence among samples of 0.002%. No differentiation was detected among the Australian localities. The New Zealand sample showed weak but significant divergence from the Australian samples. These results were similar to those from a concurrent allozyme analysis, and we conclude that there is appreciable nuclear and mitochondrial DNA gene flow among Australian localities, while the Tasman Sea separating Australia from New Zealand acts as a partial barrier.

Le tarakihi (*Nemadactylus macropterus*), un poisson marin d'intérêt commercial qui vit dans les eaux de l'Australie et de la Nouvelle-Zélande, a fait l'objet d'une détermination de la variation génétique dans le cadre d'un projet destiné à expliciter la structure des stocks. Au moyen de neuf enzymes de restriction, on a étudié la variation de l'ADN mitochondrial de 166 tarakihis capturés à proximité de sept localités du sud de l'Australie. On a pu identifier 28 haplotypes, pour une diversité haplotypique de 0,671. La diversité moyenne des nucléotides par échantillon a été calculée à 0,458 %, avec une divergence (corrigée) des nucléotides entre échantillons de 0,001 %. Aucune configuration spatiale significative n'est apparue. Cinq cents sujets provenant de huit localités du sud de l'Australie et d'une localité de la Nouvelle-Zélande ont été soumis à un examen au moyen de trois enzymes de restriction pour détecter les sites de polymorphisme soumis à un clivage. Les 33 haplotypes identifiés ont permis de fixer à 0,635 la diversité haplotypique. La diversité moyenne des nucléotides par échantillons s'élevait à 1,247 %, avec une divergence des nucléotides (corrigée) entre échantillons de 0,002 %. Nous n'avons pas pu détecter de différence en fonction des diverses localités australiennes étudiées. L'échantillon provenant de la Nouvelle-Zélande trahissait une divergence faible, mais significative par rapport aux échantillons australiens. Ces résultats s'apparentent à ceux obtenus par une analyse simultanée des allozymes. Nous parvenons à la conclusion qu'il existe un flux génétique appréciable, au niveau de l'ADN du noyau comme à celui de l'ADN mitochondrial, entre les localités de l'Australie, tandis que la mer de Tasmanie, qui sépare l'Australie de la Nouvelle-Zélande, agit comme une barrière partielle.

Received August 6, 1993
Accepted December 9, 1993
(JC039)

Reçu le 6 août 1993
Accepté le 9 décembre 1993

The jackass morwong (*Nemadactylys macropterus*) is an important commercial fish species on the continental slope of both southern Australia and New Zealand (where it is known as tarakihi). In the south east trawl fishery of Australia, which comprises those waters off Victoria, Tasmania, and southern New South Wales, about 10^6 kg per year is taken by trawling in depths of 40–350 m (Tilzey et al. 1990). The species has also been reported from the coast of Brazil and the Indian Ocean islands of Amsterdam and Saint Paul (Tong and Vooren 1972).

The commercial significance of the jackass morwong, together with the fact that a pilot study on otolith compositional variability had already been carred out (Thresher et al., unpublished), made the stock structure of this species the focus of a multidisciplinary study. This aimed to compare the utility of a number of different methods for analysing stock structure, including allozyme, mitochondrial DNA (mtDNA), meristic, and otolith chemical examination. The same inviduals were used in all studies to facilitate comparisons. To date, only the genetic components of this project have been fully analysed. The allozyme examination (Elliott and Ward 1994) failed to distinguish among Australian samples but found a New Zealand sample to have small but significantly different allele frequencies at one of eight polymorphic loci.

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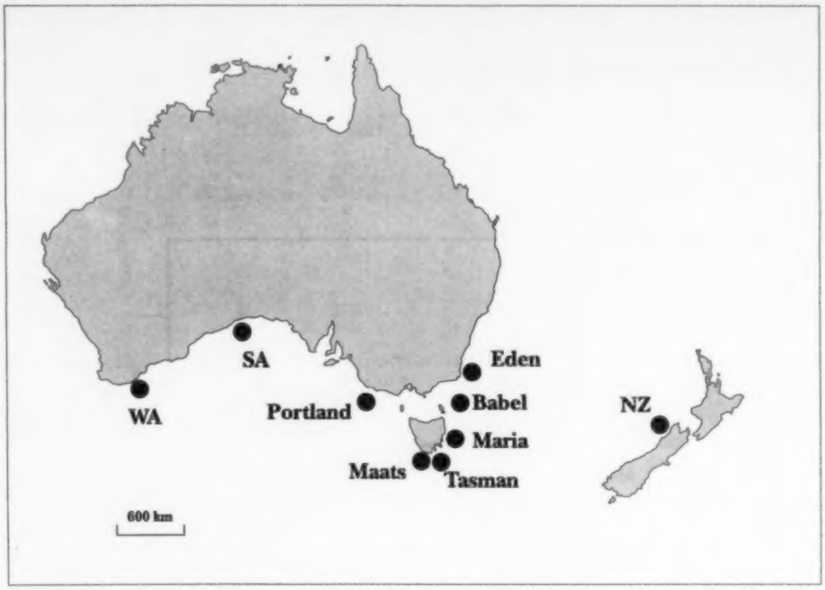

FIG. 1. Locations of samples. WA = West Australia, SA = South Australia, Maats = Maatsuyker, NZ = New Zealand. Further information about localities and sampling dates in Elliott and Ward (1994).

mtDNA analysis is generally assumed to be more powerful than allozyme analysis for revealing population structure. This is largely because mtDNA is haploid and maternally inherited: it therefore has an effective population size (assuming other factors are equal) of only one quarter that of nuclear DNA, thereby accentuating genetic drift effects (Nei and Li 1979; Birky et al. 1989). It also appears to evolve an order of magnitude faster than single-copy nuclear DNA (Brown et al. 1979; Wilson et al. 1985), although evolutionary rates in poikilotherms may be reduced (Martin et al. 1992). Yet there have been few studies of the population structures of marine fish which directly compare the resolving powers of allozyme and mtDNA analysis. Here we present the mtDNA results and compare them with the results of the allozyme analysis of the same samples (Elliott and Ward 1994).

Materials and Methods

Between January 1991 and April 1992, samples of *N. macropterus* were obtained from eight areas around southern Australia and one area off the west coast of the South Island of New Zealand (Fig. 1). Samples consisted of whole fish frozen after capture and transported to the laboratory. All fish were measured (standard length) and sexed (except the Maria Island sample), and meristic counts were taken of the dorsal, anal, and pectoral fins. Muscle, liver, and eye tissues were sampled for genetic studies and otoliths removed for chemical analysis. The tissue samples were stored at −70°C.

Total DNA was extracted from approximately 100 mg of white muscle tissue per fish by a modified CTAB (hexadecyltrimethylammoniumbromide) protocol described by Grewe et al. (1993). Nine restriction enzymes (*Bam*H I, *Ban* I, *Bcl* I, *Bst*B I, *Eco*R I, *Hind* III, *Pvu* II, *Sal* I, and *Xho* I) were used to examine 166 individuals representing seven sampling locations. As three of these enzymes (*Bam*H I, *Ban* I, and *Bcl* I) revealed more genetic variation than the remaining six, these were used to analyse 334 additional fish representing nine locations (the original seven plus two more).

Restriction fragments were separated in horizontal 1.0% agarose gels submerged in a tris-borate-EDTA (TBE) buffer system (Sambrook et al. 1989). DNA was transferred to a nylon membrane filter (Hybond N+, Amersham Ltd.) by southern transfer (Sambrook et al. 1989). The nylon membrane filters were probed with blue eye trevalla (*Hyperoglyphe antarctica*, Teleostei: Stromateoidei) mtDNA (50 ng used per ten 20 cm × 20 cm blots) purified by caesium chloride ultracentrifugation. The trevalla probe was labelled with [^{32}P]dCTP (Bresatec Pty Ltd.) by a GIGAprime DNA labelling kit (Bresatec Pty Ltd.). The membrane filters were then exposed to Kodak X-ray film for 12–48 h, routinely at −20°C without intensifying screens.

Restriction profiles for each enzyme were given letter designations in order of discovery, with the first pattern being designated "A", the second "B", and so on. Haplotypes of each fish were then identified by the combination of letters representing the restriction profiles for each restriction enzyme used.

Haplotype (nucleon) and nucleotide diversities within samples, and nucleotide diversities and divergences between samples, were computed with the REAP package (McElroy et al. 1992), using the formulations of Nei and Tajima (1981) and Nei (1987).

Chi-square analyses were used to test the null hypothesis of genetic homogeneity among samples. The Monte Carlo randomisation approach of Roff and Bentzen (1989) was used, which eliminates the need to pool rare haplotypes. Two thousand randomisations were carried out for each test.

TABLE 1. Numbers of nine-enzyme haplotypes of jackass morwong, in the order *Bam*H I, *Ban* I, *Bcl* I, *Bst*B I, *Eco*R I, *Hind* III, *Pvu* II, *Sal* I, and *Xho* I, from seven localities. *h* refers to nucleon diversity (Nei and Tajima 1981). The A+ haplotypes represent a size polymorphism (see text).

	West Australia	South Australia	Portland	Babel Island	Eden	Maria Island	Tasman Island	Total
AAAAAAAAA	9	18	12	19	16	9	10	93
AACAAAAAA	1	1	—	3	4	1	1	11
BCBAAAAAA	1	1	3	5	1	—	—	11
AACAAABAA	—	2	1	—	2	1	1	7
ABAAAAAAA	—	1	2	—	1	—	3	7
BABAAAAAA	—	—	2	—	—	3	—	5
AAAAABAAA	—	1	—	—	1	1	1	4
AAABAAAAA	1	—	—	1	—	—	1	3
AAAAAAABA	—	1	—	—	—	1	1	3
AAAAAA+A+AA	—	1	—	—	—	1	1	3
BCCAAAAAA	—	—	1	—	1	—	—	2
ABBAAABAA	1	—	—	—	—	—	—	1
AACAAAABA	1	—	—	—	—	—	—	1
DACAAAAAA	—	1	—	—	—	—	—	1
BABAAAACA	—	1	—	—	—	—	—	1
ACAAAAAAD	—	1	—	—	—	—	—	1
AAAAAAAAC	—	1	—	—	—	—	—	1
BCBAAAAAB	—	—	1	—	—	—	—	1
BABAAA+A+BA	—	—	1	—	—	—	—	1
AADAAAAAA	—	—	1	—	—	—	—	1
AACAAACAA	—	—	1	—	—	—	—	1
AACAAAACA	—	—	1	—	—	—	—	1
AACAAAAAB	—	—	—	1	—	—	—	1
CCCAAAAAA	—	—	—	—	1	—	—	1
CCAAAAAAA	—	—	—	—	1	—	—	1
AAABAA+A+AA	—	—	—	—	1	—	—	1
AAEAAAAAA	—	—	—	—	—	1	—	1
AAAAAAAAB	—	—	—	—	—	—	1	
n	14	30	26	29	29	18	20	166
h	0.604	0.646	0.782	0.547	0.687	0.745	0.747	0.671

The number of times each of the randomised replicates was greater than or equal to the observed value, divided by 2000, was an estimate of the probability of obtaining the observed value by chance.

The proportions of total genetic diversity attributable to variation among localities were estimated both by treating haplotypes as alleles, $G_{ST\text{-Nei}}$ (Nei 1973), and by considering restriction site data, $G_{ST\text{-TP}}$ (Takahata and Palumbi 1985). Sampling error alone will generate positive values of $G_{ST\text{-Nei}}$ and $G_{ST\text{-TP}}$. The magnitude of this effect was determined by bootstrapping, by taking genes at random, but with replacement, from the pooled sample while maintaining individual locality totals. Two thousand bootstrapping runs were performed for each $G_{ST\text{-Nei}}$ test and 1000 for each $G_{ST\text{-TP}}$ test. The number of times each of the bootstrapped replicates was greater than or equal to the observed value was determined. This value divided by 2000 or 1000, respectively, was an estimate of the probability of obtaining the observed or larger value by sampling error. Essentially, this tests the null hypotheses that the observed values of $G_{ST\text{-Nei}}$ and $G_{ST\text{-TP}}$ reflect sampling error alone.

Matrices of genetic distances among localities (estimated both by treating haplotypes as alleles, D_{Nei}, using Nei's (1978) distance and by considering restriction site data, D_{TP}, using Takahata and Palumbi's (1985) distance) were compared with a matrix of geographic distance. The significance of correlations were tested by Mantel's *t*-test method, as outlined by Douglas and Endler (1982).

Results

Nine-Enzyme Data

Nine restriction enzymes (*Bam*H I, *Ban* I, *Bcl* I, *Bst*B I, *Eco*R I, *Hind* III, *Pvu* II, *Sal* I, and *Xho* I) revealed 28 haplotypes among the 166 fish from seven Australian localities (Table 1). Fragment sizes are given in the Appendix. Two of these enzymes (*Hind* III and *Pvu* II) produced fragments that permitted the resolution of a 350 nucleotide base pair (bp) insertion in the mitochondrial genomes of five individuals. Given the resolution limitations of the southern blotting procedure used to visualise restriction profiles (i.e., fragments <400 bp are usually not observed), the loss or gain of a 350-bp fragment in the restriction profiles of either *Hind* III or *Pvu* II could easily explain the observed differences. However, the parallel size increase of 350 bp in both the 5300-bp *Hind* III and 4600-bp *Pvu* II restriction fragments is strong evidence for a mtDNA size polymorphism in those individuals. The mean size of the mtDNA molecule, excluding the size insertion, is 16.6 kbp. No heteroplasmic individuals were observed.

Nucleon diversity was 0.671 overall (Table 1). Chi square analysis showed no significant differentiation of haplotype numbers among these localities ($P = 0.35$). Mean nucleotide diversity per sample was 0.458%, with a mean (corrected) nucleotide divergence between pairs of samples of 0.001% (Table 2).

TABLE 2. Nucleotide diversity within and between samples, after Nei and Tajima (1981) and Nei (1987).

	Nine enzymes	Three enzymes
Nucleotide diversity per sample (%)		
Mean	0.458	1.247
Minimum	0.360	0.703
Maximum	0.645	1.499
Nucleotide diversity between pairs of samples (%)		
Mean	0.459	1.249
Minimum	0.382	0.927
Maximum	0.588	1.438
Nucleotide divergence between pairs of samples (%)[a]		
Mean	0.001	0.002
Minimum	−0.017	−0.026
Maximum	0.050	0.054

[a] This is nucleotide diversity between pairs of samples corrected for the nucleotide diversity within samples.

TABLE 3. Numbers of three-enzyme haplotypes of jackass morwong, in the order *Bam*H I, *Ban* I, and *Bcl* I, from nine localities. *h* refers to nucleon diversity (Nei and Tajima 1981).

	West Australia	South Australia	Portland	Babel Island	Eden	Maria Island	Tasman Island	Maatsuyker	New Zealand	Total
AAA	31	38	30	37	32	34	35	10	48	295
AAC	7	6	7	8	12	3	9	3	5	60
BCB	9	8	6	7	3	5	5	3	2	48
ABA	—	2	3	2	4	1	6	3	2	23
AAB	2	—	1	—	1	2	1	3	7	18
BAB	1	1	3	—	—	4	—	—	—	9
ACA	—	2	1	—	—	2	—	—	—	5
BCC	—	—	3	—	1	1	—	—	—	5
EAA	—	—	1	1	1	1	—	—	—	4
AAE	—	—	—	—	—	1	—	—	2	3
AAH	—	—	—	—	1	1	—	1	—	3
ACB	—	—	1	—	—	—	—	—	2	3
AAG	—	—	—	2	—	—	—	—	—	2
BAC	—	—	—	—	1	—	1	—	—	2
CCC	—	—	—	—	1	1	—	—	—	2
ABB	1	—	—	—	—	—	—	—	—	1
DAC	—	1	—	—	—	—	—	—	—	1
AAD	—	—	1	—	—	—	—	—	—	1
AFA	—	—	1	—	—	—	—	—	—	1
AAI	—	—	—	1	—	—	—	—	—	1
BCF	—	—	—	1	—	—	—	—	—	1
FAA	—	—	—	1	—	—	—	—	—	1
ADA	—	—	—	—	1	—	—	—	—	1
BAA	—	—	—	—	1	—	—	—	—	1
CCA	—	—	—	—	1	—	—	—	—	1
AEA	—	—	—	—	—	1	—	—	—	1
CCB	—	—	—	—	—	1	—	—	—	1
EAC	—	—	—	—	—	1	—	—	—	1
AAF	—	—	—	—	—	—	1	—	—	1
BAE	—	—	—	—	—	—	1	—	—	1
EAB	—	—	—	—	—	—	1	—	—	1
BFC	—	—	—	—	—	—	—	1	—	1
AAJ	—	—	—	—	—	—	—	—	1	1
n	51	58	58	60	60	59	59	24	71	500
h	0.578	0.547	0.710	0.595	0.677	0.660	0.616	0.793	0.529	0.635

Three-Enzyme Data

Five hundred fish from eight Australian localities and one New Zealand locality were analysed with each of the three restriction enzymes *Bam*H I, *Ban* I, and *Bcl* I that detected polymorphic cut sites.

These three enzymes identified 33 haplotypes (Table 3).

TABLE 4. Probabilities from chi-square analysis (Roff and Bentzen 1989) of pairwise sample comparisons of haplotype numbers based on three restriction enzymes and 2000 Monte Carlo iterations. Probabilities less than 5% are given; probabilities greater than 5% are given as n.s. (not significant).

	South Australia	Portland	Babel Island	Eden	Maria Island	Tasman Island	Maatsuyker	New Zealand
West Australia	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.025	0.012
South Australia	—	n.s.	n.s.	n.s.	n.s.	n.s.	0.014	0.004
Portland	—	—	n.s.	n.s.	n.s.	n.s.	n.s.	0.006
Babel Island	—	—	—	n.s.	n.s.	n.s.	0.037	0.003
Eden	—	—	—	—	n.s.	n.s.	n.s.	0.005
Maria Island	—	—	—	—	—	0.026	n.s.	0.034
Tasman Island	—	—	—	—	—	—	n.s.	0.009
Maatsuyker	—	—	—	—	—	—	—	n.s.

TABLE 5. Comparison of $G_{ST\text{-Nei}}$ analyses between the allozyme and mtDNA data, treating the mtDNA haplotypes as alleles. $G_{ST\text{-Nei (null)}}$ values, which are those derived from 2000 bootstrapped replications, represent the levels of $G_{ST\text{-Nei}}$ that can be attributed to sampling error alone.

	All nine sites			Australian (pooled) vs. New Zealand		
	$G_{ST\text{-Nei}}$	$G_{ST\text{-Nei (null)}}$	P	$G_{ST\text{-Nei}}$	$G_{ST\text{-Nei (null)}}$	P
mtDNA	0.0230	0.0178	0.130	0.0126	0.0043	0.024
*sAAT-1**	0.0214	0.0058	0.003	0.0446	0.0014	<0.001
Eight polymorphic allozymes[a]	0.0064	0.0058	0.269	0.0046	0.0014	0.002

[a] From Elliott and Ward (1994).

Haplotype AAA predominated (59% over all samples), followed by AAC (12%), BCB (9.6%), ABA (4.6%), AAB (3.6%), BAB (1.8%), and ACA and BCC (1%). The 25 remaining haplotypes each had frequencies of less than 1%. Nucleon diversity ranged from 0.529 (New Zealand) to 0.793 (Maatsuyker). Mean nucleotide diversity per sample was 1.247%, and mean (corrected) nucleotide divergence between pairs of samples was 0.002% (Table 2).

The first set of analyses considered haplotypes as alleles. Chi-square analysis showed that these haplotypes were not distributed randomly with respect to locality ($P = 0.0135$). In order to identify the source of this heterogeneity, all possible pairwise comparisons of localities were carried out (Table 4). Eleven of these 36 tests were significant at the 5% level. Although none of these was significant after applying the (conservative) Bonferroni correction procedure for multiple tests ($\alpha = 0.05$, adjusted $\alpha = \alpha/36 = 0.0014$), seven of the 11 comparisons with $P < 0.05$ were comparisons of New Zealand with Australian localities. The eighth New Zealand comparison yielded $P = 0.064$. Furthermore, the five comparisons with probabilities less than 0.01 were five of the eight comparisons between New Zealand and Australian localities. There was also some suggestion that the Maatsuyker sample might be different from other samples, with three pairwise comparisons with other Australian samples having probabilities less than 0.05 (but greater than 0.01) and the New Zealand comparison having a P value of 0.064. When each sample in turn was compared with all other samples pooled, only the New Zealand sample was distinguishable at the 5% level (West Australia, $P = 0.810$; South Australia, 0.811; Portland, 0.272; Babel Island, 0.104; Eden, 0.188; Maria Island, 0.075; Tasman Island, 0.536; Maatsuyker, 0.339; New Zealand, 0.023).

This suggests that the significant heterogeneity among localities detected in the first test was primarily attributable to differentiation of the New Zealand sample. Removing this sample and testing for haplotype heterogeneity among the eight Australian samples alone gave a nonsignificant result ($P = 0.104$). These analyses therefore indicated that the New Zealand sample was significantly different from the Australian samples, while the Australian samples did not differ significantly among themselves. Much of this heterogeneity was attributable to the AAB haplotype, which had a frequency of 0.113 in the New Zealand sample but only 0.023 in the pooled Australian sample. When this haplotype was eliminated, the comparison of the pooled Australian sample versus the New Zealand sample was not significant ($P = 0.132$).

About 2% of the total haplotype variation was attributable to variation among the nine localities ($G_{ST\text{-Nei}} = 0.023$, Table 5), but this was not significantly greater than that attributable to sampling error alone ($P = 0.13$). Pooling the Australian localities and comparing this pooled sample with the New Zealand sample reduced the proportion of variation arising from locality differences to about 1% ($G_{ST\text{-Nei}} = 0.013$), but this is greater than that arising from sampling error alone ($P = 0.024$). After allowing for sampling error, the corrected value of $G_{ST\text{-Nei}}$ equates to around 0.008, which in turn equates, at equilibrium, to around 60 female migrants per generation. This calculation uses Wright's (1943) relationship between G_{ST} and $N_e m$, modified for mtDNA data, giving $G_{ST} = 1/(1 + 2N_e m_f)$. In this equation, N_e is the effective population size and m_f the female migration rate.

Nei's (1978) unbiased genetic distances were estimated for all pairwise sample comparisons by treating the mtDNA haplotypes as alleles. A UPGMA-derived dendrogram separated the New Zealand sample from the others (Fig. 2), although there was no significant relationship between D_{Nei} and geographic distance between pairs of localities ($r = 0.342$, $t = 1.41$, $P > 0.05$).

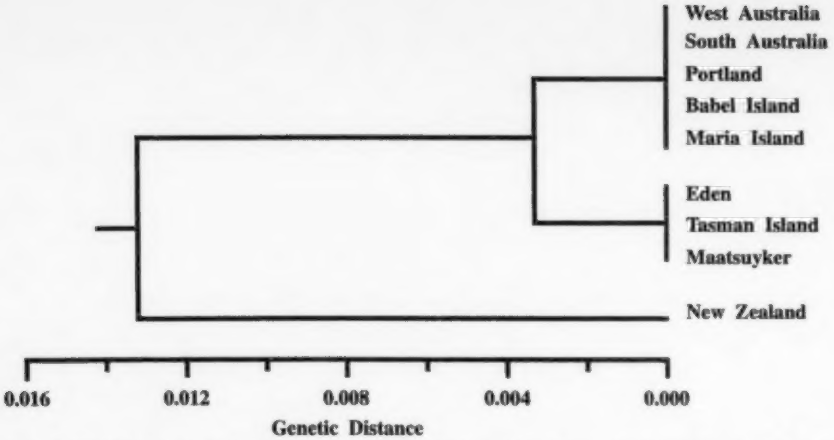

FIG. 2. UPGMA-derived dendrogram of Nei's (1978) unbiased genetic distance among localities, considering the haplotypes as alleles.

TABLE 6. Pairwise sample comparisons of restriction site data, after Takahata and Palumbi (1985). Identity probabilities within localities (I) on diagonal (bold), identity probabilities between localities (J) above diagonal, distances (D_{TP}) below diagonal. Mean $I = 0.680$, mean $J = 0.626$, mean $D_{\mathrm{TP}} = 0.083$.

	West Australia	South Australia	Portland	Babel Island	Eden	Maria Island	Tasman Island	Maatsuyker	New Zealand
West Australia	**0.749**	0.699	0.653	0.583	0.701	0.648	0.706	0.703	0.665
South Australia	0.035	**0.699**	0.614	0.552	0.657	0.610	0.662	0.658	0.627
Portland	0.066	0.093	**0.650**	0.522	0.616	0.574	0.621	0.656	0.589
Babel Island	0.125	0.145	0.165	**0.583**	0.554	0.546	0.589	0.554	0.561
Eden	0.035	0.065	0.093	0.145	**0.703**	0.612	0.664	0.661	0.628
Maria Island	0.067	0.093	0.117	0.113	0.093	**0.641**	0.654	0.612	0.620
Tasman Island	0.035	0.064	0.092	0.090	0.064	0.033	**0.713**	0.665	0.673
Maatsuyker	0.033	0.065	0.031	0.146	0.063	0.094	0.064	**0.705**	0.629
New Zealand	0.069	0.094	0.120	0.114	0.095	0.061	0.033	0.095	**0.678**

A second set of analyses (Table 6) considered the patterns of restriction site variation among haplotypes across all nine localities, using the formulae of Takahata and Palumbi (1985). $G_{ST\text{-}\mathrm{TP}}$ was estimated at 0.135, which implies that about 13% of the restriction site variation was attributable to geographic differentiation. However, of 1000 bootstrapped values, this value was equalled or exceeded on 457 occasions ($P = 0.457$). Thus the observed $G_{ST\text{-}\mathrm{TP}}$ value, although apparently quite large, is not significantly greater than that assignable to sampling error alone. Comparing the pooled Australian samples with the New Zealand sample gives a similarly nonsignificant result ($G_{ST\text{-}\mathrm{TP}} = 0.124$, $P = 0.180$). These analyses, therefore, fail to confirm the significant heterogeneity shown by the chi-square haplotype analysis. We suspect that the poorer resolution of the restriction site analysis is because most of the restriction sites are shared among haplotypes, while the haplotypes themselves are unique. There was no significant relationship between genetic distance among restriction sites (D_{TP}, see Table 6) and geographic distance between pairs of localities (Mantel test, $r = 0.184$, $t = -0.684$, $P > 0.05$).

Discussion

Nucleon diversity (h) of the jackass morwong at around 0.67 for the nine-enzyme analysis is similar to that of the bluefish (*Pomatomus saltatrix*) ($h = 0.696$, Graves et al. 1992a) and yellowfin tuna (*Thunnus albacares*) ($h = 0.724$, Ward et al. 1994a). Some marine fishes have nucleon diversities approaching the maximum attainable of 1.0 (e.g., red drum (*Sciaenops ocellatus*), $h = 0.94$, Gold and Richardson 1991; Atlantic menhaden (*Brevoortia tyrannus*), $h = 0.99$, Bowen and Avise 1990); others are around 0.90 (e.g., haddock (*Melanogrammus aeglefinus*), $h = 0.87$, Zwanenburg et al. 1992; Atlantic herring (*Clupea harengus*), $h = 0.91$, Kornfield and Bogdanowicz 1987), while some are well below those of jackass morwong (e.g., Atlantic cod (*Gadus morhua*), $h = 0.36$, Carr and Marshall 1991, $h = 0.10$, Smith et al. 1989; American plaice (*Hippoglossoides platessoides*) $h = 0.35$, Stott et al. 1992; weakfish (*Cynoscion regalis*), $h = 0.16$, Graves et al. 1992b). However, nucleon diversity is a crude measure of variability. It is based on haplotype frequencies alone, and as more restriction enzymes are employed in a study and additional variable cut sites detected, the number of haplotypes and therefore the value of h increases. The mean nucleotide diversity per jackass morwong sample is 0.458% for the nine-enzyme study and 1.247% for three-enzyme study (which selected those restriction enzymes that revealed the most genetic variation).

This study focussed on the mtDNA haplotype distribution of the 500 fish characterised by the restriction enzymes *Bam*H I, *Ban* I, and *Bcl* I. Haplotype numbers in New Zealand fish were different from those in Australian fish ($P = 0.023$), while Australian samples, despite spanning a coastline of about 3000 km, were not different from each other (P = 0.104). However, the degree of difference between these two sets of samples was small and primarily attributable to frequency differences in a single haplotype (AAB). The overall similarity of fish from the Australian – New Zealand region was supported by a G_{ST}-based analysis of restriction site diversity, which failed to demonstrate significant differentiation among samples. The mean nucleotide divergence between pairs of samples, having corrected for diversity within samples, was 0.002% for the three-enzyme study.

It therefore seems probable that there is gene flow among jackass morwong populations throughout this region, with the Tasman Sea between Australia and New Zealand acting as a partial barrier. This conclusion is supported by the lack of significant correlations between genetic and geographic distances and the observation that 14 of the 15 haplotypes recorded more than once were found in two or more localities. The exceptional haplotype was AAG, found in only two fish, both off Babel Island. While this might represent a remnant of population structuring, it is more likely to be a chance occurrence. Thus, there is very little evidence of haplotypes being restricted to single localities, although much larger sample sizes would be required to evaluate this hypothesis for the many rare haplotypes.

How does these findings accord with those of the allozyme analysis (Elliott and Ward 1994)? While the mtDNA analysis showed the jackass morwong to have levels of mtDNA diversity, *h*, around the mean for marine fishes, the average allozyme heterozygosity per locus (0.101) was estimated to be about twice the mean of other marine fishes (around 0.05, Smith and Fujio 1982; Ward et al. 1994b). However, both analyses concluded that there was a lack of genetic differentiation among the Australian localities, but there was significant, if minor, differentiation of the New Zealand sample. The allozyme differentiation was primarily attributable to variation at one of eight polymorphic loci, *sAAT-1**, where the common allele had a frequency of around 0.80 in the Australian samples and 0.95 in the New Zealand sample (Elliott and Ward 1994).

The haploid, maternally inherited nature of mtDNA should make it a more powerful tool for examining population subdivision than the allozymes coded by nuclear DNA (e.g., Avise et al. 1979; Lansman et al. 1983; Saunders et al. 1986; Ward et al. 1989; Reeb and Avise 1990; but see Ferguson et al. 1991; Ward et al. 1994a). However, in the jackass morwong study the allozyme approach arguably provided more evidence for population subdivision than did the mtDNA analysis. For example, with respect to chi-square analysis, the probabilities of no significant differentiation between the New Zealand sample and the pooled Australian sample were 0.001 for alleles at the *sAAT-1** locus, 0.011 for a combined probability across all eight polymorphic allozymes (Elliott and Ward 1994), and 0.023 for mtDNA haplotypes. Furthermore, while the mtDNA $G_{ST\text{-Nei}}$ values are about three times greater than the eight allozyme data (Table 5), much of this is attributable to the increased sampling error associated with the mtDNA analysis; the probability that the allozyme $G_{ST\text{-Nei}}$ comparison between the pooled Australian samples and the New Zealand samples arises by chance is in fact an order of magnitude smaller than that derived from the mtDNA comparison (P = 0.002 and 0.024, respectively). The greater variance of the haplotype than allozyme $G_{ST\text{-Nei}}$ values to a large extent reflects the substantially smaller sample size used in the former analysis. Only 500 mitochondrial DNA alleles, with a genetic diversity of 0.635, were examined, compared with nearly 1800 nuclear alleles (880 fish) for each of eight independent allozyme loci, with heterozygosities or genetic diversities ranging from 0.237 to 0.592 per allozyme (Elliott and Ward 1994). However, we are not arguing that one approach should be preferred over the other: both have advantages and disadvantages, and their joint application to studies of population structure will always be more powerful than the application of a single approach.

In our case, the congruence of the two data sets gives added confidence that there was indeed significant differentiation of the New Zealand sample from the Australian samples. The allozyme data taken over the eight polymorphic loci indicated about 80 migrants per generation between New Zealand and Australia (Elliott and Ward 1994), a figure similar to the mtDNA estimate of around 60 females per generation. It should be stressed that both these figures are very approximate estimates. Not only do they have large standard errors, but they assume, for example, that populations are at equilibrium and that selection is not operating.

Other genetic studies have compared marine species from New Zealand and south east Australian waters, and several of these have suggested that the Tasman Sea is a partial barrier to gene flow. Allozyme data from blue grenadier (*Macruronus novaezelandiae*) parallel the jackass morwong results closely. No significant genetic differences were observed among samples from three localities off southeastern Australia, while there were small but significant differences across the Tasman Sea (Milton and Shaklee 1987). The snapper (*Chrysophrys auratus*) similarly showed allozymic differentiation across the Tasman Sea (MacDonald 1980). Limited mtDNA data from the rock lobster (*Jasus verreauxi*) were also suggestive of trans-Tasman Sea differences, although more extensive data from *Jasus edwardsii* failed to show such differentiation (Ovenden et al. 1992; Brasher et al. 1992).

While our data indicate mixing among Australian localities, the extent of this mixing is uncertain. A tagging study off the New South Wales coast, based on 69 recaptured fish, indicated little movement of adults over one year (Smith 1989). However, a more extensive New Zealand tagging programme carried out over several years indicated that an appreciable proportion of adult jackass morwong do move long distances and that some may spawn in different areas in successive years (Annala 1993). Larval and prejuvenile drift may be another important factor promoting genetic homogeneity. The jackass morwong has an 8- to 10-mo offshore pelagic postlarval period, followed by metamorphosis to a bottom-living juvenile resembling the adult in form (Tong and Vooren 1972; Vooren 1972, 1975). In Australian waters, the availability of the Leeuwin Current in the west and south and the East Australian Current (with associated eddies) in the east means that gene flow resulting from larval drift over several months could equal or exceed that resulting from adult migrations.

Our data indicate that New Zealand fish form a separate genetic stock from Australian fish, but the failure of the analysis to reject the null hypothesis of genetic homogeneity of Australian jackass morwong does not necessarily mean that Australian jackass morwong constitute a single panmictic unit. It remains possible that several genetic stocks are present in Australian waters, but that our analysis failed to uncover their existence. Since we examined eight polymorphic allozymes in 780 fish, and 33 mtDNA haplotypes in 429 fish (numbers which exlude the New Zealand sample), from samples covering a 3000-km coastline, any such genetic differentiation is likely to be very limited. Nevetheless, the observed levels of homogeneity could be maintained by levels of gene flow ranging from high to quite low, and therefore the extent of self-recruitment remains unknown. Given this uncertainty, a conservative approach to management of the jackass morwong is warranted, pending further information on the number and extent of spawning areas and nursery grounds, recruitment processes, and migration rates.

Acknowledgements

This work was supported by grant 91/32 from the Fishing Industry Research and Development Trust Fund. We thank Peter Smith (MAF, Wellington, New Zealand) for arranging collection and shipment of jackass morwong (tarakihi) from New Zealand and Neil Billington, Nick Elliott, Ron Thresher, Vivienne Mawson, and an anonymous referee for comments on an earlier version of this paper.

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Appendix. Restriction Fragment Lengths (kbp) of the Different Haplotypes

*Bam*H I					
A	B	C	D	E	F
—	—	16.6	—	—	—
—	—	—	—	11.1	—
—	13.9	—	—	—	—
8.4	—	—	—	—	—
—	—	—	7.8	—	—
5.5	—	—	5.5	5.5	5.5
—	—	—	—	—	4.5
—	—	—	—	—	4.0
2.7	2.7	—	2.7	—	2.7
—	—	—	0.6	—	—
16.6	16.6	16.6	16.6	16.6	16.7

Ban I					
A	B	C	D	E	F
9.4	9.4	9.4	—	—	9.4
—	—	—	—	7.6	—
—	—	—	5.2	—	—
—	—	—	4.2	—	—
3.5	—	3.5	3.5	3.5	—
—	2.8	—	—	—	2.8
—	—	2.3	—	—	2.2
2.1	2.1	—	2.1	2.1	—
1.9	1.9	1.9	1.9	1.9	1.9
—	—	—	—	1.8	—
—	0.7	—	—	—	0.7
0.2	0.2	—	0.2	0.2	—
17.0	17.0	17.0	17.0	17.0	17.0

Bcl I									
A	B	C	D	E	F	G	H	I	J
—	—	—	—	—	—	—	14.5	—	—
—	—	—	—	—	—	—	—	—	14.3
12.2	—	—	—	12.2	—	—	—	—	—
—	—	—	10.6	—	—	10.6	—	—	—
—	—	—	—	—	—	—	—	10.4	—
—	8.2	8.2	—	—	8.2	—	—	—	—
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
—	4.1	4.1	—	—	4.1	—	—	4.1	—
—	—	—	—	—	3.3	—	—	—	—
2.2	2.2	—	2.2	—	—	—	—	—	2.2
2.0	2.0	2.0	2.0	2.0	—	2.0	2.0	2.0	—
—	—	—	1.6	—	—	1.6	—	—	—
—	—	1.3	—	1.3	—	1.3	—	—	—
—	—	1.0	—	1.0	1.0	1.0	—	—	—
16.5	16.5	16.5	16.5	16.5	16.5	16.5	16.5	16.5	16.5

*Bst*B I	
A	B
14.5	—
—	8.0
—	6.6
2.1	2.1
16.6	16.7

*Eco*R I	
A	B
16.6	—
—	9.6
—	7.0
16.6	16.6

Hind III		
A	A+	B
—	5.7	—
—	—	5.6
5.3	—	5.3
4.5	4.5	—
3.8	3.8	3.8
1.1	1.1	1.1
1.1	1.1	—
0.6	0.6	0.6
16.4	16.8	16.4

Pvu II			
A	A+	B	C
5.8	5.8	5.8	—
—	5.0	—	—
4.6	—	4.6	4.6
3.4	3.4	3.4	3.4
—	—	—	3.4
—	—	—	2.4
1.7	1.7	—	—
1.4	1.4	1.4	1.4
—	—	1.0	1.0
—	—	0.7	0.7
16.9	17.3	16.9	16.9

Xho I			
A	B	C	D
11.4	11.4	11.4	—
—	—	—	6.5
—	—	—	4.9
—	2.7	—	—
2.0	—	2.0	2.0
—	—	1.7	—
1.3	1.3	—	1.3
0.7	0.7	0.7	0.7
0.6	—	0.6	0.6
0.4	0.4	—	0.4
16.5	16.5	16.5	16.5

Chela Function, Morphometric Maturity, and the Mating Embrace in Male Snow Crab, *Chionoecetes opilio*

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Claxton, W.T., C.K. Govind, and R.W. Elner. 1994. Chela function, morphometric maturity, and the mating embrace in male snow crab, *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 51: 1110–1118.

Behavior and chela function associated with precopulatory clasping in morphometrically mature (MM) and morphometrically immature (MI) male snow crab, *Chionoecetes opilio*, were compared. MM males clasp receptive females more readily and for a more protracted period than MI males. Moreover, smaller MM males were more successful in initiating and maintaining precopulatory holds than larger MI males. These differences in clasping behavior cannot be attributed to differences in chela function, as the force developed is sufficient for clasping in both cases. The output force of the MM chela is, however, significantly higher than for MI chela because of their higher mechanical advantage and muscle stress and the presence of a larger closer muscle. Nor are differences in clasping behavior due to the fiber composition of the chela closer muscle which is composed of slow fibers in both morphotypes. These fibers are highly differentiated in their sarcomere lengths and enzymatic (ATPase and NADH-diaphorase) profiles which allow them to provide slow, powerful, and sustained contractions suited to precopulatory clasping. Since chela morphology and closer muscle composition appear adapted to precopulatory clasping in both morphotypes, other factors, most likely neurohormonal, may make MM males clasp more readily than their MI conspecifics.

On a comparé le comportement et la fonction des chélipèdes lors de l'étreinte précopulatoire chez des mâles du crabe des neiges, *Chionoecetes opilio*, qui ont atteint leur maturité morphologique (MM) ou non (MI). Les mâles MM étreignent les femelles réceptives plus volontiers et pour plus longtemps que les mâles MI. En outre, les mâles MM de plus petite taille ont plus de succès que les mâles MI plus gros pour prendre et garder les femelles dans une étreinte précopulatoire. Ces différences de comportement d'étreinte ne peuvent pas être attribuées à des différences au niveau du fonctionnement des chélipèdes puisque la force développée est suffisante pour maintenir l'étreinte chez tous les sujets. Toutefois, la force produite par les chélipèdes des MM est significativement supérieure à celle produite par les chélipèdes des MI; cela est attribuable à un avantage mécanique, une plus forte tension musculaire et de plus gros muscles de fermeture des chélipèdes. On ne peut pas, non plus, attribuer les différences dans le comportement d'étreinte à la composition en fibres du muscle de fermeture des chélipèdes, qui est composé de fibres à contraction lente dans les deux types morphologiques. Ces fibres sont très différenciées sur le plan de la longueur des sarcomères et sur le plan des profils enzymatiques (ATPase et NADH-diaphorase), qui rendent possibles des contractions lentes, puissantes et soutenues qui favorisent l'étreinte précopulatoire. Puisque la morphologie et que la composition des muscles de fermeture des chélipèdes paraissent adaptées à l'étreinte précopulatoire chez les deux types morphologiques, d'autres facteurs, fort probablement neurohormonaux, peuvent aider les mâles MM à étreindre plus spontanément les femelles que leurs congénères MI.

Received July 13, 1993
Accepted November 23, 1993
(JC005)

Reçu le 13 juillet 1993
Accepté le 23 novembre 1993

Snow crab, *Chionoecetes opilio* (Brachyura, Majidae), support important fisheries in the Northwest Atlantic, the Bering Sea, and the Sea of Japan (Bailey and Elner 1989). However, fundamental biological criteria to distinguish reproductive capability and maturity for *Chionoecetes* species are not well established (Somerton 1981; Elner and Beninger 1989, 1992). In eastern Canada, the legal minimum size of 95 mm carapace width (CW) was designed to restrict snow crab landings to mature males; females attain a maximum size of only 47–95 mm CW. Early observations on gonad development, presence of spermatophores, and chela allometry suggested that all males attain maturity between 51 and 75 mm CW (Watson 1970). Growth was presumed to continue past maturity; consequently, males were assumed to have at least one opportunity to copulate before being fished (Elner and Bailey 1986). However, reexamination of this premise indicates that for *C. opilio* in the Northwest Atlantic, at least, the molt at which chelae undergo allometric growth is a terminal molt (O'Halloran 1985;

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Conan and Comeau 1986; Conan et al. 1989). As for other majids (Hartnoll 1963), the implications are that male snow crab can cease growth over a wide size range, between approximately 50 and 159 mm CW, and are not fully mature before terminal molt (Elner and Beninger 1992). Nonetheless, males that have not attained terminal molt can have fully formed spermatophores in their vas deferens (Beninger et al. 1988) and may copulate in some circumstances (Conan et al. 1989; Ennis et al. 1990).

Allometric growth of the male chelae at the terminal molt results in subtle changes in chelae shape and relative size (Fig. 1), which, in turn, provide a means to distinguish morphological types. Logarithmic plots of chela size versus CW show separation between regression lines for morphometrically immature (MI) males and morphometrically mature (MM) males in, supposedly, terminal anecdysis (Conan and Comeau 1986). These external changes in chelal dimensions have been surmised to indicate functional changes, allowing a MM male to grip the base of a hard-shelled, multiparous female's walking legs for several weeks prior to copulation, through copulation and subsequent egg extrusion (Conan and Comeau 1986; Elner and Beninger 1992). Laboratory observations (Watson 1970, 1972) and recent field studies (Sainte-Marie and Hazel 1992) indicate that mating of primiparous females also involves protracted male grasping. Govind et al. (1992) determined that the chela closer muscle and its motor patterns and excitatory neuromuscular synapses are specialized for slow, sustained activity, such as an extended precopulatory embrace in both MI and MM male snow crab.

Premises on terminal molt, criteria to determine maturity, and the ramifications for snow crab fisheries management are still being debated (Jamieson and McKone 1988; Elner and Beninger 1989; Safran et al. 1990; Dawe et al. 1991; Sainte-Marie and Hazel 1992). Here we compare aspects of precopulatory behavior, chela mechanics, and muscular properties between MM and MI male snow crab in an effort to resolve aspects of the current controversy.

Materials and Methods

Snow crab were collected near Pinnacle Rock, Bonne Bay, Newfoundland, between May 18 and June 23, 1990. Males for examination of chelal mechanics were captured by either trawl or traps at approximately 90 m depth. These crabs were transported to Nova Scotia and held in running seawater at the Halifax Fisheries Research Laboratory, before being air-freighted to Scarborough College, Ontario. There they were maintained in recirculating seawater at 4°C and used within a month of their arrival. Male and female crabs, for behavioral studies and in vivo force measurements, were taken by SCUBA divers from depths of 4–40 m and kept in seawater at the Memorial University Marine Station, Bonne Bay. They were held for less than 2 wk before being used and were not fed. In these males, the shell condition was noted not only for its hardness but also for the presence of epiphyte growth along the margins of the shell. Only hard-shelled males in intermolt condition C_4 to D_0 (O'Halloran and O'Dor 1988) were used, as mating has not been reported for premolt or early postmolt stages (Watson 1970; Hooper 1986). Also, early postmolt male crabs exhibited poor mobility and little force in dactyl closing, making them poor subjects for experimentation.

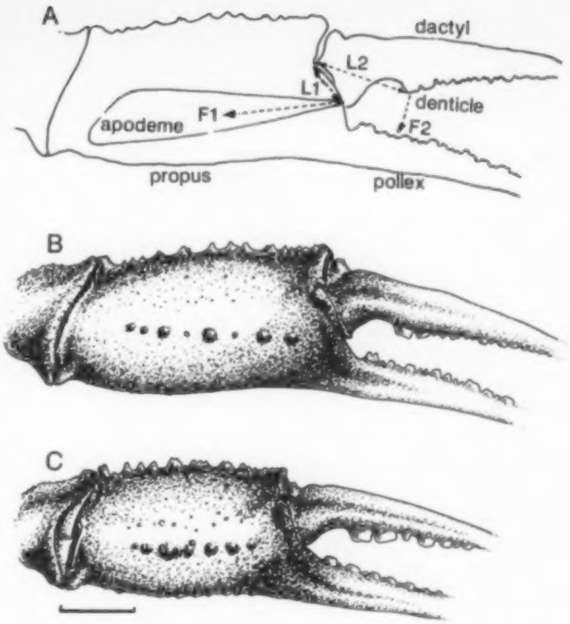

FIG. 1. (A) Chela of male snow crab showing the forces (F) and levers (L) involved in the closing action. (B and C) Representative chela from MM and MI males, respectively; both crabs 88 mm CW. Scale bar: 10 mm.

All crabs were tagged with an identification number and their CW and chela height measured to the nearest millimetre with vernier calipers. Only female carrying eyed-eggs were used, as others were not receptive to males. Males were designated as either MM or MI based on the equation (Conan and Comeau 1986)

$$Y = -0.788931 \ln CW + 0.61448 \ln \text{chela height} + 1.76051.$$

Male crabs of Y greater than zero are MM; crabs are MI when Y is less than zero. The equation is estimated to be 99% effective in distinguishing the two morphs.

Behavior

Two behavioral studies were made of crabs in tanks (90 × 50 × 40 cm) with flowing seawater at ambient temperature (4–5°C) at the Bonne Bay Marine Station. Crabs were used once and then released.

First, observations of individual male/female pairs were made four times daily (08:00, 12:00, 18:00, and 23:00) over 5-min periods. At these times, details of the clasping behavior, if such behavior occurred, were noted such as where the female was held and by which chela. A total of 32 pairs were observed; 17 involved MM males and 15 MI males.

Second, observations were made of competitions between a small (70–85 mm CW) MM male and a large (90–100 mm CW) MI male for a female. Observations were made for 5 min each at the following times: 08:00, 12:00, 18:00, and 23:00. An experiment was terminated when one male maintained the female in an embrace for three consecutive observation periods. A total of 10 competitions were recorded.

TABLE 1. Clasping behavior of MM and MI male snow crab.

	MM	MI
No. observed	17	15
No. initiated clasping	17	8
No. initiated clasping in first observation period (4 h)	17	4
No. maintaining clasp until eggs extruded	16	2
No. copulating	5	0

Functional Morphology

Functional basis to male clasping behavior was examined by analysing chelal mechanics and properties of chela closer muscle for MM and MI males.

Mechanical advantage (MA)

Crustacean chelae are operated by a lever system (Warner and Jones 1976). In a system with frictionless pivots:

$$F1 \times L1 = F2 \times L2$$

where F1 is force applied to the system (i.e., through contraction of the closer muscle) and F2 is force produced (i.e., the closing action). L1 and L2 are the levers along which these forces act and represent the shortest distance between the hinge and lines of action of the respective forces (Fig. 1). Mechanical advantage (MA) is the factor by which the magnitude of the F1 is altered; because the chela hinge has little friction, MA may be estimated by the ratio of lever lengths L1/L2. Thus, F2 increases with MA, although the speed of any movement and distance moved both decrease in proportion. L1 was measured between the hinge and the point of attachment of the apodeme of the closer muscle. L2 is commonly described as the distance between the hinge and the tip of the dactyl. However, as the female's legs are pinched by the large bicuspid first denticle, we considered the effective L2 to be between this latter point and the hinge.

Muscle force and stress

Closing force (F2) was measured in vivo for 25 males. For each, the right chela was immobilized and the central dactyl tooth attached by a short length of nonelastic cord to a linear spring balance. The crab was induced to close its dactyl by stroking the inside of the pollex with a brush. Closing force (F2) was then estimated by pulling vertically upwards on the spring balance until the dactyl began to open. Individual crabs were subjected to three or four such measurements over a 15-min period; only the most forceful measurement for each was retained.

Muscle stress (S), contractile force generated per unit area of the closer muscle, was estimated for each crab from the equation (Alexander 1983)

$$S = \mathrm{F1}/A \sin 0.$$

Apodeme area (A), an index of the maximum longitudinal area of the closer muscle, was calculated from tracings of the outlines of apodemes on a computer image analysis system. The angle of pinnation (0) of the closer muscle fibers was measured from tracings of the dorsal surface of the muscle fibers onto the apodeme using a camera lucida.

Muscle composition

A morphological and two histochemical methods were used to characterize fibers from the chela closer muscle. For the morphological method, sarcomere length (SL) of myofibrils was measured; SL is directly related to contractile speed (Atwood 1976). The closer muscle was fixed, in situ, in a relaxed state by holding the dactyl open while Bouin's fluid was injected into the muscle through the exoskeleton. Fixing was continued by immersing the cheliped in Bouin's for 3 d after which it was stored in 70% ethanol. Fibers were sampled by dividing the muscle transversely into proximal, central, and distal sections. Within each section, eight samples were taken: two dorsally, four centrally, and two ventrally. For each sample, three separate measurements were made each consisting of six sarcomeres in series and three A-bands. A-bands are less subject to length changes than myofibrils (Franzini-Armstrong 1970) and served to verify that the sarcomeres were not unduly stretched or contracted. Measurements of SL and A-band lengths were made to the nearest micrometre using phase contrast objectives and an ocular micrometer (Govind et al. 1986). A total of 432 sarcomeres and 216 A-bands were measured for each closer muscle. In total, muscles from four MM males and four MI males were examined.

For the first histochemical method, activity of an enzyme, myofibrillar ATPase, was assessed (Ogonowski and Lang 1979). Differential staining for ATPase reflects differences in specific activity of this enzyme related to contractile speed; fast fibers have a higher specific activity than slow (Hajek et al. 1973). The exoskeleton of the chela was filed down with a hobby drill to expose the hypodermis, before the cheliped was covered with an embedding medium (optimal cutting temperature compound by Tissue Tek) and frozen by immersion in 2-methylbutane cooled in liquid nitrogen. Next, the chela was cut transversely into proximal, central, and distal regions. Cross-sections (20 μm) from each region were obtained by standard techniques (Govind et al. 1986). Sections were air dried on glass coverslips for 15 min before being incubated for 30 min at 4°C in an ATPase medium consisting of 0.05 M glycglycine, buffered at pH 8.0 with KOH, 18 mM $CaCl_2$, 1.5 M MgCl, and 3 M ATP. This was followed by a series of rinses in water and 1% $CaCl_2$ and by an incubation in 2% $CoCl_2$. Next, sections were water rinsed, incubated in 1% ammonium sulphide, and again rinsed in water before being dehydrated in ethanol, cleared in xylene, and mounted on glass slides.

For the second histochemical method, oxidative capacity of muscle fibers was determined by staining frozen cross-sections for NADH-diaphorase, an enzyme located principally in the mitochondria. Sections were incubated in the dark for 2 h, at room temperature, in a 0.05 M phosphate buffer (pH 7.5) containing 0.98 mM nitro-blue tetrazolium and 0.97 mM NADH. After rinsing in water, sections were dehydrated in ethanol, cleared in xylene, and mounted on glass slides. Both histochemical methods were used in each of 30 closer muscles of which 15 muscles were from MM and 15 from MI males.

Results

Behavior

Our observations on clasping or embracing of a female snow crab by a male crab associated with copulation confirm and extend earlier findings (Watson 1970, 1972). The male, using his chelae, initially grasped the female from any angle, at any available site on her appendages or carapace. In the next few minutes, the male manipulated the female into a face-to-face position by grasping her legs on one side with one of his chelae. This position was maintained over the majority of the holding period. Although the general form of the mating embrace appeared similar between MM and MI males, there were differences in clasping behavior between these two morphs (Table 1). Thus, all 17 MM males demonstrated clasping compared with 8 of the 15 MI males, a significant difference ($\chi^2 = 10.15$, df = 1, $p < 0.01$). Moreover, all MM males initiated clasping within the first observation period as compared with four of the eight MI males ($\chi^2 = 19.0$, df = 1, $p < 0.001$). All but one of the 17 MM males retained the female until egg extrusion, in comparison with 2 of 15 MI males. Copulation, defined as insertion of the male's pleopods into the female's genital openings, was observed in 5 of the 17 MM pairings but in none of the 15 MI cases. The interval between copulation and egg extrusion in the five MM males ranged between 6 and 24 h for a mean of 15.6 h.

In 8 of 10 competitive trials, a small MM male gained possession of the female and retained her in the presence of the larger MI male for the entire observation period. The large MI male was successful in 2 of 10 trials. Hence, small MM males were successful more often than their large MI counterparts ($\chi^2 = 7.2$, df = 1, $p < 0.01$). Behavior of MM and MI males differed; upon introduction into the test tank, the small MM male immediately seized the female whereas the large MI male showed sporadic interest in the female by advancing and retreating from her. Also, once clasping had been established by the small MM male, no attempts to break this hold were made by the large MI male. Conversely, the small MM male repeatedly attempted to break clasping by the large MI male.

Functional Morphology

Gross chelal morphology of the two male morphs appears virtually indistinguishable to the casual observer (Fig. 1). The occluding surfaces of the dactyl and pollex are lined by a number by small tubercles. The most prominent amongst these is a single large bicuspid first denticle on the dactyl with a matching socket on the pollex. In a closed chela the occluding surfaces of the first denticle meet.

Mechanical advantage

Mean MA (±SE) values for MM (0.427 ± 0.032; $n = 14$) and MI (0.350 ± 0.032; $n = 15$) males were different ($t = 4.64$, df = 28, $p < 0.05$). Regression of lever length against CW (Fig. 2) shows that L1 is elevated in MM as compared with MI crabs ($t = 7.923$, df = 27, $p < 0.05$). Consequently, a differential increase in L1 at the molt to morphometric maturity is mainly responsible for differences in MA between the two morphs. Paradoxically, however, the regression for L2 was also significantly elevated in MM compared with MI crabs ($t = 3.850$, df = 27, $p < 0.05$) (Fig. 2); here, the higher L2 values would act to lower MA.

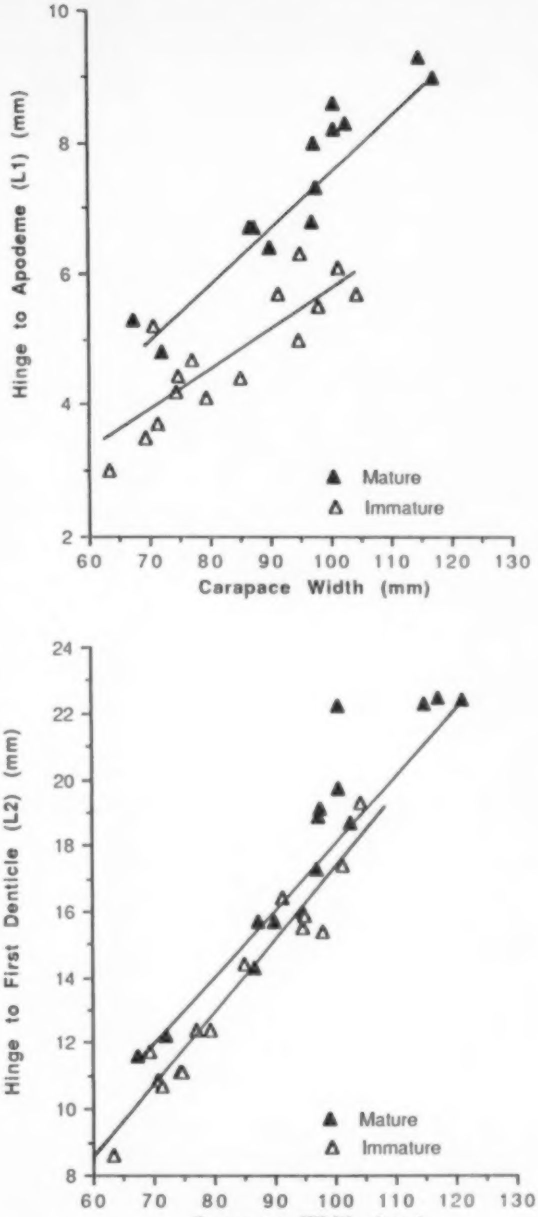

FIG. 2. Relationship between CW and length of levers, L1 (upper) and L2 (lower), in the chela of MM (solid triangles) and MI (open triangles) male snow crab. The relationship between L1 (y) and CW (x) is expressed by the regression line $y = -1.564 + 0.094x$ for MM crabs ($n = 13$) and $y = -0.344 + 0.061x$ for MI crabs ($n = 15$). The regression line for L2 (y) and CW (x) is $y = -3.88 + 0.277x$ for MM crabs ($n = 14$) and $y = -4.92 + 0.227x$ for MI crabs ($n = 31$).

Force and stress

Apodeme area, an index of the closer muscle area, was larger for MM males than for MI males of a given CW ($t = 7.67$, df = 2, $p < 0.05$) (Fig. 3). Because this indicated that MM crabs have allometrically larger chela closer muscles,

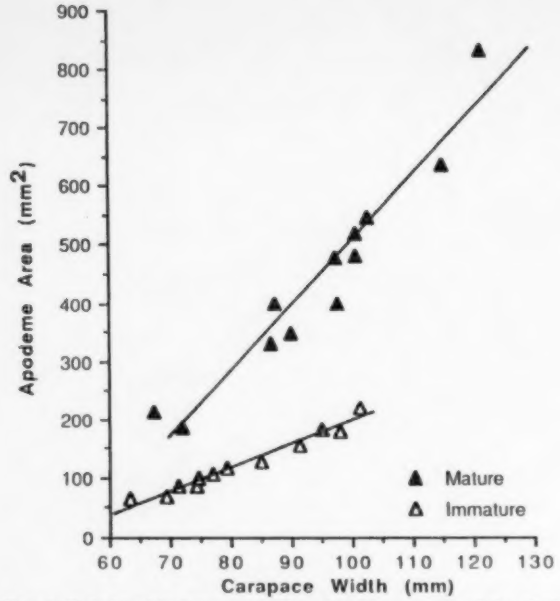

FIG. 3. Relationship between CW and apodeme area of the chela closer muscle in MM (solid triangles) and MI (open triangles) male snow crab. The regression line for apodeme area (y) and CW (x) is $y = -599.96 + 11.029x$ for MM crabs ($n = 12$) and $y = -199.24 + 3.951x$ for MI crabs ($n = 13$).

recorded muscle forces were expressed relative to apodeme area. This allowed a comparison of forces in MM and MI closer muscles of equal size. The maximum force developed by the muscle itself (F1) was greater for MM than MI chela closer muscles ($t = 2.72$, df = 22, $p < 0.05$) (Fig. 4). Likewise, the force of closing of the dactyl (F2) was also greater for MM than for MI males ($t = 4.00$, df = 22, $p < 0.05$) (Fig. 4). This difference between MM and MI males in terms of F2 may be due to superior mechanical advantage of the MM chela. However, bearing in mind that MM males have a much larger closer muscle than their MI counterparts (Fig. 3), the output force (F2) for MM males is severalfold greater than for MI males for crabs with comparable CW.

A further comparison between MM and MI crabs was made in terms of contractile force per unit area of the closer muscle, i.e., stress. The mean maximum stress for MM muscle was 0.552 N/mm^2 ± 0.024 ($n = 12$) and for MI muscle was 0.444 N/mm^2 ± 0.029 ($n = 13$), a significant difference ($t = 2.88$, df = 25, $p < 0.05$).

Muscle composition

SLs of myofibrils were measured from closer muscles of four MM and four MI male snow crab. The pattern of distribution of SLs is essentially similar between the two morphs, as shown by a representative example from each category (Fig. 5). Fibers are of a wide range of SLs, 4–17 μm, and bimodally distributed, with the first mode at 4–6 μm and the second mode at 12–13 μm.

Measurements of A-bands, which are less subject to variations than myofibrils (Franzini-Armstrong 1970), were also made. The A-band data parallel those of the SL, in that they show a wide range from 2 to 9 μm and are bimodal, 3–4 and 7–8 μm (Fig. 5). Thus, the closer muscle is composed of two populations of fibers differing in SL and, hence, contractile properties. To determine if the populations are distributed in a regional fashion within the muscle, SL data

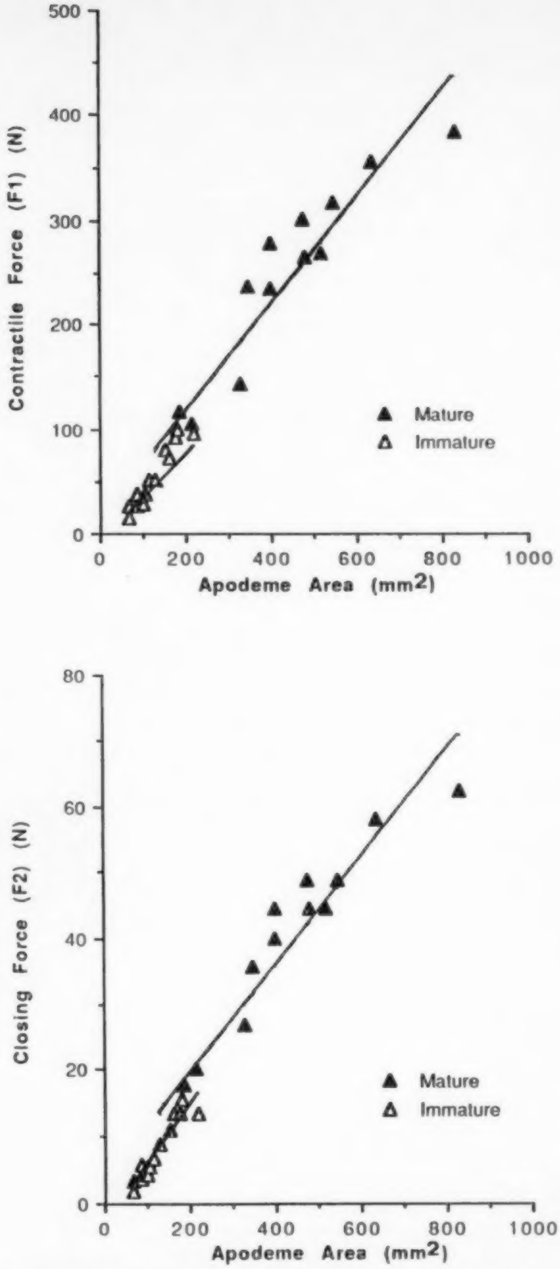

FIG. 4. Relationship between apodeme area of the chela closer muscle and contractile force (F1) (upper) and closing force (F2) (lower) in MM (solid triangles) and MI (open triangles) male snow crab. The regression line for F1 (y) and apodeme area (x) is $y = 43.920 + 0.462x$ for MM crabs ($n = 12$) and $y = -19.167 + 0.586x$ for MI crabs ($n = 13$). The regression line for F2 (y) and apodeme area (x) is $y = 8.22 + 0.073x$ for MM crabs ($n = 12$) and $y = -3.12 + 0.090x$ for MI crabs ($n = 13$).

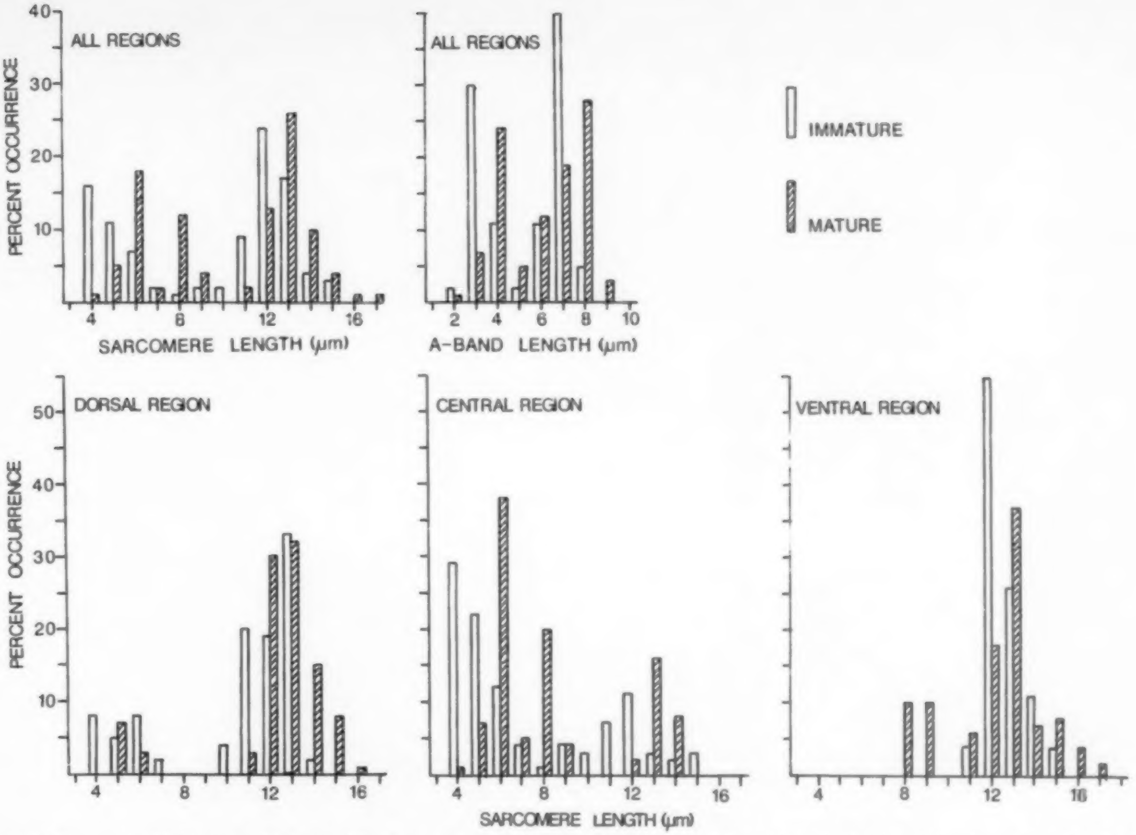

FIG. 5. Frequency histogram of fibers with characteristic sarcomere lengths and A-band lengths in the chela closer muscle of a MI (open bars) and MM (hatched bars) male snow crab shown for the entire muscle (upper) and for different regions (lower); n = 513 sarcomeres (133 dorsal, 239 central, 141 ventral) and 232 A-bands for MI and 481 sarcomeres (122 dorsal, 233 central, 126 ventral) and 283 A-bands for MM.

were analysed based on the area from which the fibers were sampled (i.e., dorsal, central, and ventral region) (Fig. 5). A similar pattern emerged for both MM and MI muscles. The dorsal region contains predominantly long SL fibers, the central region has almost the reverse pattern with mostly short SL fibers and a few long SL ones, and the ventral region has only long SL fibers.

In cross-sections of chelae treated histochemically for detecting myofibrillar ATPase, there was variation in staining intensity between fibers, especially in the proximal and middle regions of the muscle (Fig. 6). Most muscle sections stain in a fairly uniform dark manner, although lighter-staining fibers appear in the dorsal and ventral areas. Fibers in the distal region stain more uniformly. The pattern of staining was similar in both MM and MI males.

Muscle fibers stained either intensely or lightly for NADH-diaphorase and in a distinctly regional manner (Fig. 6). Intensely stained fibers occur as a broad band in the middle of the cross-sections from proximal and middle regions with lightly staining fibers bisecting this band as well as sandwiching it between the dorsal and ventral sides. Fibers in the ventral region appear uniformly lightly stained. Both MM and MI males showed similar staining patterns.

Discussion

Chelae can be considered "ecological templates" in that the life style of a crab species is uniquely reflected in its chelal morphology (Elner 1980). The phenomenon of differentiation of snow crab chelae at the molt to morphometric maturity is seen variously as a key to understanding the terminal molt premise (Conan and Comeau 1986), defining "maturity" (Conan et al. 1989), and a means for regulating the commercial fishery (Safran et al. 1990; Tremblay et al. 1992). Here we assess the functional role of snow crab chelae as a secondary sexual characteristic.

Our behavioral comparisons demonstrate clear differences between the propensities of MI and MM males to clasp and retain multiparous females. These findings support laboratory (Conan and Comeau 1986; Moriyasu and Conan 1988) and field (Taylor et al. 1985; Hooper 1986; Ennis et al. 1988, 1990) observations suggesting that MI males do not usually engage in multiparous mating. Also, recent field surveys in the northwestern Gulf of Saint Lawrence found MI males to be uncommon in sexual pairs with pubescent females (Sainte-Marie and Hazel 1992). We provide data on the interval between copulation and egg extrusion. How-

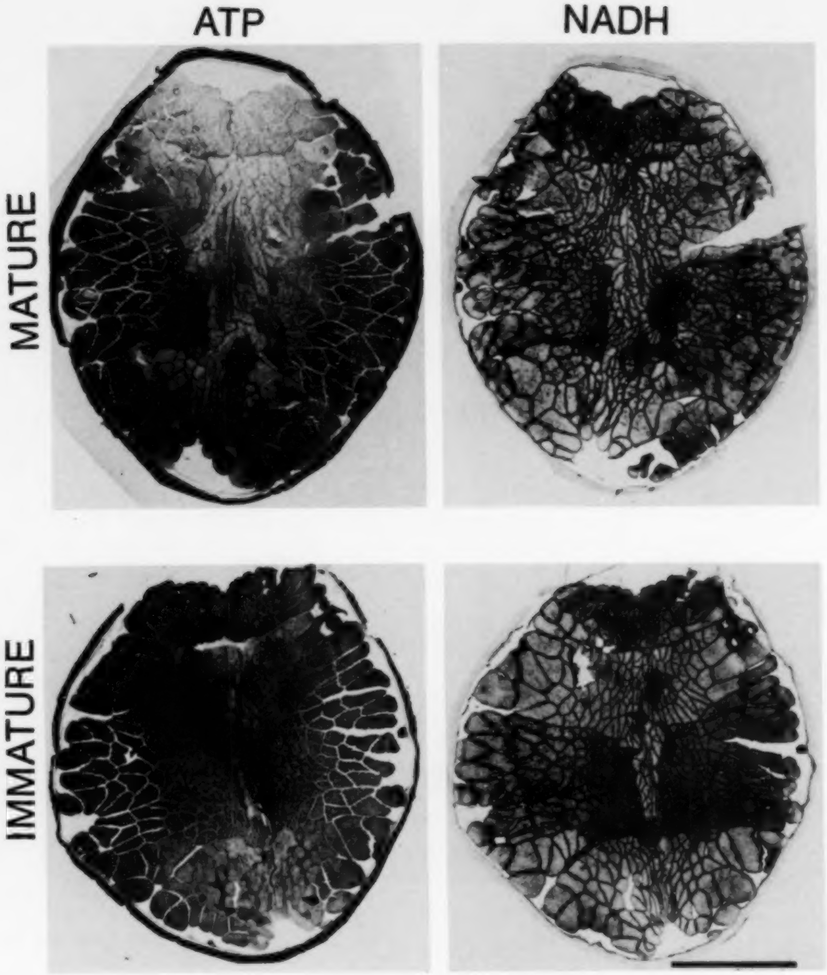

FIG. 6. Adjacent frozen cross-sections stained for myofibrillar ATPase and NADH-diaphorase activity from the midregion of the chela of a MM male and a MI male. The large, bipinnate closer muscle with a tendon down the midline occupies most of the cross-sectional area of the claw, while the small, also bipinnate opener muscle is restricted to the extreme dorsal or upper retion. Scale bar: 5 mm.

ever, although such information has not previously been recorded for multiparous female snow crab, the fertility of the eggs was not ascertained and the possibility that females may have utilized stored sperm remains (Elner and Beninger 1992; Beninger et al. 1993).

We investigated morphological, mechanical, and physiological properties of chelae from both male morphs in an attempt to explain differences in mating behavior. The functional implications of the various allometric and biomechanical differences detected between chelae of the two morphs are uncertain. For example, the chelae of the MM males have a relatively higher mechanical advantage which, coupled with their relatively larger closer muscles and higher stress capabilities, indicates that they can develop bigger output forces than chelae of MI males of comparable CW. However, the output force capabilities of chelae of MI males, although generally only approximately 30% of similar sized MM males, are comparable with estimates for other decapod species (Brown et al. 1979; Elner 1980; Elner and Campbell 1981). Thus, the functional basis to the distinction remains enigmatic. Although there are marked mechanical differences, in terms of relative size, closer muscle stress, and maximum force capability, between the two chela types, these do not appear by themselves to either necessarily preclude MI males from maintaining a mating embrace or explain why they do not. Indeed, other functional aspects of the chelae, such as gross morphology, muscle fiber composition, and motor firing patterns (Claxton 1992; Govind et al. 1992), appear similar in the two morphs. Hence, the original question, "can a MI male hold a multiparous female in a mating embrace?" is modified to "why does a MI male not hold a multiparous female in a mating embrace?"

While differences in F2 are not necessarily a factor in mating ability, muscular composition and innervation are, but these appear identical between the two morphs. The fiber composition of the closer muscle determines the strength and duration of its contraction (Jahromi and Atwood 1969). Traditionally, crustacean muscle fibers have been classified according to their contractile speed, with mean SL providing a convenient index of speed; fast fibers have short SLs of 2–4 μm and slow fibers have longer SLs of >4 μm (Govind and Atwood 1982). Chela closer muscles from MM and MI male snow crab are strikingly similar in their SLs, which range from 4 to 13 μm, making the muscles essentially slow. However, within this category of slow muscle, there is considerable variation in both MI and MM crabs; about a third are clustered around a SL mode of 4–6 μm and the remaining two thirds around a longer SL mode of 12–13 μm. Overall, evidence from characters investigated suggests that chelae from both MM and MI males can develop slow powerful contractions suitable for clasping. Closer muscles with a similar SL distribution are seen in several other crustaceans, e.g., in the chelae of blue crab (Govind and Blundon 1985), fiddler crab (Rhodes 1986), and crayfish (Govind and Pearce 1985) and in the major chela of American lobster (Lang et al. 1977) and snapping shrimp (Stephens and Mellon 1979). In all these cases, there is a wide range in contractile activity of the slow type. Fast-type contractions are seen in the closer muscle of the minor chela of lobsters in which most of the fibers have SLs of 2–4 μm with the result that closing movements can occur as rapidly as 20 ms.

Differentiation in structural properties of the muscle is complemented by differences in the activities of two enzymes, ATPase and NADH-diaphorase. The former regulates the speed of contraction based on its specific activity and the latter is directly related to muscle fatigability. Histochemical detection of these enzymes revealed several staining intensities for each, demonstrating that there are several different activity levels for these enzymes in the chela closer muscle. Thus, a combination of structural and enzymatic properties endows the closer muscle with considerable versatility in its contractile behavior; but behavior where the emphasis is on slow, forceful, and prolonged contractions, suitable for maintaining a mating embrace, occurs in both MM and MI males.

A hypothesis to explain why otherwise mechanically capable MI males do not readily grasp receptive females invokes modulation of synaptic activity at both the periphery and in the central nervous system by circulating amines and peptides. Neurohormonal regulation of behavior is dramatically seen in the octopamine-regulated alert posture (limbs and abdomen extended) and the serotonin-regulated submissive posture of American lobster (Kravitz 1988). Moreover, behavioral regulation within a molt cycle by bloodborne factors is implicated in the tendency of premolt lobsters to display threat by meral spread (Schwanke et al. 1990). Similar factors at the molt to morphometric maturity in male snow crab may trigger the expression of precopulatory clasping. Support for the hypothesis comes from studies suggesting that juvenile hormone, methyl farnesoate, regulates not only differentiation of chelae but also the state of the reproductive system in different male morphs of another majid, *Libinia emarginata* (Homola et al. 1991).

To account for the allometric growth causing morphological and mechanical differences between chelae of the two male morphs, we hypothesize that female choice and/or intermale competition during the precopulatory phase has produced strong selective forces for the augmented male characteristics, chela size and strength, observed in MM males. A similar argument was advanced for the relatively larger chelae of male, as compared with female, American lobster (Elner and Campbell 1981). If our neurohormonal hypothesis is correct and MI males can be experimentally induced to display MM behavior, the latter hypothesis could be tested by repeating our competition experiments with the addition of MI males modified with MM hormones. If modified MI males were outcompeted by MM males of the same CW, the hypothesis would stand; conversely, the hypothesis could be dismissed should the modified MI males perform as well as their MM conspecifics.

Acknowledgements

We are indebted to R.G. Hooper for the use of facilities at the Memorial University Marine Station, Norris Point, Newfoundland, and for his expert and helpful advice. John Guchardi provided technical assistance in field and laboratory studies and Lynn Lee produced Fig. 1B and 1C. This research was funded by a Science Subvention Grant, administered jointly by the Department of Fisheries and Oceans and the Natural Sciences and Engineering Research Council of Canada, and by a research grant from the latter to C.K.G.

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Use of a Stereo-video System to Estimate the Energy Expenditure of Free-swimming Fish

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Krohn, M.M., and D. Boisclair. 1994. Use of a stereo-video system to estimate the energy expenditure of free-swimming fish. Can. J. Fish. Aquat. Sci. 51: 1119–1127.

We tested the ability of a stereo-video method to provide estimates of the metabolic costs of spontaneous swimming by simultaneously video taping free-swimming fish and measuring their oxygen consumption. Three swimming characteristics (speed, turning rate, and acceleration) obtained from image analysis of video recordings explained, on average, 80% of the variability in spontaneous swimming costs. Colinearity among the swimming characteristics prevented us from estimating their relative importance. We converted the swimming speeds recorded by the stereo-video system to metabolic costs using relationships from the literature between oxygen consumption and speed during forced swimming (swimming with constant speed and direction). Spontaneous swimming costs, measured directly by respirometry, were, on average, six times higher than the costs predicted by the forced swim relationships for the same speeds. This difference suggests that the metabolic costs of turning and acceleration can be substantial. Relationships used to convert movements obtained with the stereo-video method into energy expenditure should therefore be developed using spontaneously swimming fish and should include turning rate and acceleration as well as speed.

Nous avons testé l'habileté de la méthode stéréo-vidéo pour estimer les coûts métaboliques de la nage spontanée en filmant la nage des poissons et en mesurant simultanément leur consommation d'oxygène. Les trois caractéristiques de nage (la vitesse, le taux de virage et l'accélération) obtenues avec la méthode stéréo-vidéo ont expliqué, en moyenne, 80 % de la variabilité des coûts de nage spontanée. La colinéarité entre les caractéristiques de nage nous a empêché d'estimer leur importance relative. Nous avons converti les vitesses de nage enregistrées par le système stéréo-vidéo en coûts métaboliques à l'aide d'une relation dérivée de données disponibles dans la littérature entre la consommation d'oxygène et la vitesse de nage forcée (nage à vitesse et direction constantes). Les coûts de nage spontanée mesurés directement par respirométrie ont été en moyenne six fois plus grands que les coûts prédits par une relation décrivant les coûts de la nage forcée pour les mêmes vitesses. Cette différence suggère que les coûts associés aux virages et aux accélérations peuvent être substantiels. Les relations utilisées pour convertir les mouvements obtenus en dépense énergétique devraient être développées en utilisant la nage spontanée et devraient inclure les virages et les accélérations en plus de la vitesse.

Received May 11, 1993
Accepted December 8, 1993
(JB927)

Reçu le 11 mai 1993
Accepté le 8 décembre 1993

Fish bioenergetic models have been used to study the dependence of energy allocation patterns on environmental conditions (Adams et al. 1982; Wieser and Medgyesy 1991) and to predict growth rates (Rice et al. 1983; Diana 1987; Brandt et al. 1992), mortality rates (Johnson and Evans 1991), population biomass (Stewart et al. 1983), and impact of predators on prey abundance (Kitchell and Breck 1980; Majkowski and Waiwood 1981). The metabolic cost of activity (e.g., costs associated with migration, escape, and foraging) has been recognized as a weak link in fish energy budgets (Kitchell et al. 1977; Adams et al. 1982; Soofiani and Hawkins 1985; Weatherley and Gill 1987; Lucas et al. 1991). While it is believed to be important to account for the magnitude and variability of activity costs (Boisclair and Leggett 1989; Boisclair and Sirois 1993; Hansen et al. 1993; Madon and Culver 1993; Ney 1993), obtaining direct in situ estimates is logistically difficult.

Boisclair (1992a) demonstrated that the stereo-video method can provide accurate estimates of in situ swimming speed, turning rate, and acceleration of small fish from sequentially recorded fish positions. To quantify energy expenditure associated with activity, speeds can be converted to energy cost using laboratory-determined relationships. For a wide range of species, metabolic cost – swimming speed relationships have been determined from the oxygen consumption of fish forced to swim against a current of water flowing at a series of controlled velocities (forced swimming; Beamish 1980). There is empirical and theoretical evidence, however, that the costs associated with forced swimming substantially underestimate the cost of free or spontaneous swimming (Webb 1991; Boisclair and Tang 1993). The difference in cost between forced and spontaneous swimming has been attributed to the inability to account for the costs associated with changes in speed and direction in forced swimming experiments. Transformation

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TABLE 1. Conditions for experiments in which spontaneous swimming costs and fish swimming characteristics were estimated.

Exp.	Temp. (°C)	Aquarium dimensions (cm)	Aquarium volume (L)	No. of fish	Mean fish weight (g)	Fish density ($g \cdot L^{-1}$)	Mean total length (cm)
1	11.0	60 × 30 × 30	54	8	5.2	0.76	8.4
2	12.5	30 × 30 × 30	27	4	7.9	1.2	9.7
3	12.0	120 × 30 × 30	108	16	9.7	1.4	10.4
4	12.0	60 × 30 × 30	54	8	8.6	1.3	10.0
5	12.0	60 × 30 × 30	54	16	8.1	2.4	9.8
6	12.0	60 × 30 × 30	54	4	7.5	0.55	9.5
7	11.0	30 × 30 × 30	27	4	8.9	1.3	10.1

of movements observed using the stereo-video system into energy expenditure may therefore require the development of relationships between metabolic swimming costs and a more complete series of swimming characteristics including turning rate and acceleration as well as speed.

Our objectives are (1) to experimentally evaluate whether forced swimming costs adequately represent those of spontaneous swimming and (2) to examine how much of the variability in the metabolic costs of spontaneous swimming can be explained by three swimming characteristics: speed, turning rate, and acceleration.

Methods

We evaluated whether forced swimming costs accurately represent the energetic costs of activity in free-swimming fish by examining the relationship between the cost of spontaneous swimming and the cost of swimming predicted by forced swim models at the same speeds. Spontaneous swimming costs were measured directly with respirometry. Forced swimming costs associated with observed speeds were estimated indirectly from published forced swimming speed – metabolic cost relationships (Brett 1964, 1965).

To determine whether speed, turning rate, and acceleration obtained with the stereo-video system could be used to accurately estimate the energetic costs of activity of free-swimming fish, we developed relationships between oxygen consumption and swimming characteristics by analyzing images acquired from stereo-video recordings.

Experimental Design

Spontaneous swimming costs and fish swimming characteristics were estimated simultaneously during seven experiments. Different swimming patterns (i.e., a range in speed, acceleration, and turning rate) were obtained by varying aquarium size and fish density. Aquarium volumes were 27, 54, and 108 L and fish densities ranged from 0.55 to 2.4 $g \cdot L^{-1}$ (Table 1). Aquarium size and fish density were not varied to permit us to use test volume and density effects on activity levels, but rather to generate variability in swimming characteristics to allow for a relationship predicting spontaneous swimming costs. Experiments were performed using brook trout (*Salvelinus fontinalis*), weighing from 5 to 11 g wt.

Experimental Procedure

Spontaneous swimming costs

Spontaneous swimming costs were estimated from oxygen consumption in hermetically sealed Plexiglas aquaria, hereafter referred to as respirometers. The respirometers were placed inside a 500-L Living Stream aquarium (model LSW 700) to maintain a constant temperature. The temperature ranged from 11 to 12.5°C among experiments (Table 1).

Fish were not fed for 3 d prior to the experiments and were allowed to stabilize in the respirometer during the last 24 h. During the stabilization, water was pumped through the respirometer to avoid oxygen depletion. At the onset of the experiment, water circulation was turned off and oxygen concentration was measured by a probe inside the respirometer. The dissolved oxygen meter (YSI model 57) was calibrated using the unmodified Micro Winkler method (APHA 1985). Biological oxygen demand of the water (BOD) was estimated from the decrease in oxygen concentration of water in a 1-L sealed clear glass bottle placed in the water next to the respirometer during the experiment. BOD ranged from 6 to 20% of total oxygen depletion.

Activity levels of brook trout at 12°C have been found to depend on oxygen concentrations below 7.6 mg $O_2 \cdot L^{-1}$ (Graham 1949). The experiments were stopped after the oxygen concentration in the respirometer decreased by 1 mg $O_2 \cdot L^{-1}$ to avoid reaching subcritical levels. Oxygen concentration never dropped below 9.0 mg $O_2 \cdot L^{-1}$. Experiments lasted between 2.6 and 6 h. Experiment length was not significantly related to oxygen consumption of individual fish ($p > 0.2$).

Fish were weighed individually at the end of each experiment (±0.01 g wet). Length was determined from a length–weight relationship for brook trout (D. Boisclair, unpublished data).

Swimming characteristics

The fish were video-taped while swimming in the respirometer through a glass window (0.3 × 1.5 m) in the side panel of the Living Stream aquarium. The video camera system consisted of two Panasonic WV-BL602 cameras, equipped with Cosmicar automatic iris EX-2 lenses, mounted in parallel, 10 cm apart. A Panasonic Quad WJ-450 received the images from both cameras and ensured temporal synchrony between them. Time of day (hours:minutes:seconds) was supplied by a time-day camera titler (TDCT) and added to the images processed by the Quad. From the TDCT the images were sent simultaneously to a television monitor and a Sony EV-C3 video cassette recorder. The use of two cameras allowed for the estimation of fish position in three dimensions (Boisclair 1992a).

Positioning of a fish requires the estimation of the distance between the optical axes of the two cameras. The separation of optical axes will either decrease or increase with the distance from the cameras because the cameras can never be perfectly parallel. A relationship between target distance and optical axes separation was obtained by filming rulers placed in a respirometer at known distances from the cameras.

Recorded images were analyzed using Jandel Video Analysis Software (Java). Fish positions, determined at 1-s intervals, were defined by four pairs of coordinates: the *x*- and *y*-coordinates obtained for the head and tail of the fish on both images.

Fish were defined as either "swimming" or "resting" to avoid the necessity of taking positions of resting fish. A fish was considered to be resting when it moved less than 0.5 $cm \cdot s^{-1}$ (0.05 body $length \cdot s^{-1}$) for three or more consecutive seconds. A speed of 0.5 $cm \cdot s^{-1}$ is associated with negligible oxygen consumption (<5% of standard metabolism). The underestimation of oxygen consumption of "resting fish" due to the cutoff speed should be considerably less than 5% because the resting fish were, for the most part, motionless. Each experiment was viewed from beginning to end to determine the proportion of time fish spent swimming.

Boisclair (1992a) found that while the number of movements analyzed in a 2-m^3 enclosure did not influence average speed values, the range was affected and stabilized when the sample size reached 100–150. We assessed the influence of sample size in our aquaria by taking 1000 estimates of swimming speed from one experiment and estimating speed using subsamples of 50, 100, and 200 speeds. The range of speeds increased with sample size. The range covered by a sample size of 200 represented 99.6% of that included by the sample of 1000 estimates. A sample size of 200 was therefore considered sufficient to adequately describe swimming speed. The 20 series of 11 consecutive positions analyzed during each experiment were distributed evenly throughout the duration of the experiment.

Computations

Spontaneous swimming costs

Total oxygen depletion was determined from the difference in oxygen concentration at the beginning and the end of an experiment. Routine metabolic rate of the fish (i.e., including standard metabolism) (C_R; milligrams O_2 per gram per hour) was calculated as

$$(1)\quad C_R = (\Delta[O_2] - \mathrm{BOD}) \cdot V/W$$

where $\Delta[O_2]$ (milligrams O_2 per litre per hour) is total oxygen depletion in the water, BOD (milligrams O_2 per litre per hour) is the biological oxygen demand of the water, *V* (litres) is the volume of the respirometer, and *W* (grams) is the total weight of all fish in the respirometer. Oxygen consumption due exclusively to activity (i.e., spontaneous swimming) (C_s; milligrams O_2 per gram per hour) was calculated as

$$(2)\quad C_s = C_R - \mathrm{SMR}$$

where SMR (milligrams O_2 per gram per hour) is standard metabolic rate. Standard metabolism was interpolated from graphs of brook trout SMR as a function of temperature and weight (Job 1955).

Swimming characteristics

Head and tail speed were determined from their change in position over a 1-s time interval as described in Boisclair (1992a). Swimming speed (centimetres per second) was calculated as the average speed of the head and tail. Acceleration (centimetres per second per second) was estimated as the difference in swimming speed between two successive 1-s intervals. Turning rate (*T*; degrees per second) was estimated from the difference in position of the head relative to the tail between time *t* and *t* + 1 (Boisclair 1992b).

Forced swimming costs

Relationships between oxygen consumption and swimming speed have not been determined for small brook trout (<10 g), but have been extensively studied for sockeye salmon (*Oncorhynchus nerka*) across a broad range of sizes and temperatures. We have used sockeye salmon forced swimming costs in the present study because the forced swimming costs of brook trout are almost identical to those of sockeye salmon of the same weight (Beamish 1980). Combining data from Brett (1964, 1965), we obtained the following relationship between metabolic cost of forced swimming excluding standard metabolism (C_f; milligrams O_2 per gram per hour), swimming speed (Sw; centimetres per second), weight (*W*; grams), and temperature (*T*; degrees Celsius):

$$(3)\quad \ln C_f = 0.72 \ln W + 1.36 \ln \mathrm{Sw} + 0.45 \ln T - 6.55$$
$$R^2 = 0.98;\ p < 0.0001;\ n = 51.$$

In the data set used to develop the equation, fish weight ranged from 3 to 1400 g, speed ranged from 0 to 160 $cm \cdot s^{-1}$, and temperature ranged from 5 to 15°C. For each experiment the forced swimming cost associated with each of the observed 200 speeds was calculated with equation (3). The average cost was then multiplied by the proportion of time the fish spent swimming.

Swimming cost ratio

Swimming cost ratio (SCR) can be defined as the ratio of the metabolic cost of spontaneous swimming to that of forced swimming for a given set of speeds (Boisclair and Tang 1993). SCR was calculated for each experiment as

$$(4)\quad \mathrm{SCR} = C_s/C_f$$

where C_s and C_f are, respectively, the average spontaneous and forced swimming costs for the particular experiment.

Data Analysis

Spontaneous swimming costs

The 95% CI associated with each estimate of spontaneous swimming costs was determined from the instrumental error associated with oxygen concentration measurements (±0.05 mg $O_2 \cdot L^{-1}$). The error associated with each oxygen consumption estimate, because it was based on four oxygen readings (before and after in both the respirometer and BOD bottle), was ±0.2 mg $O_2 \cdot L^{-1}$. We assumed that the instrumental error was normally distributed around 0. One thousand error values were randomly chosen from this distribution ($\bar{x} = 0$; SD = 0.2) and added to a spontaneous cost to create a distribution of 1000 pseudo-spontaneous costs. The 95% CI of a spontaneous swimming cost was defined as being limited by 2.5th and 97.5th percentile of that distribution.

Spontaneous swimming costs among experiments were compared using a permutation procedure. For each of 999 permutations, the 7000 pseudo-spontaneous costs (1000 pseudo-spontaneous costs for each of the seven experiments) were randomly divided into seven groups of 1000. A test statistic (*Q*) was obtained for each permutation:

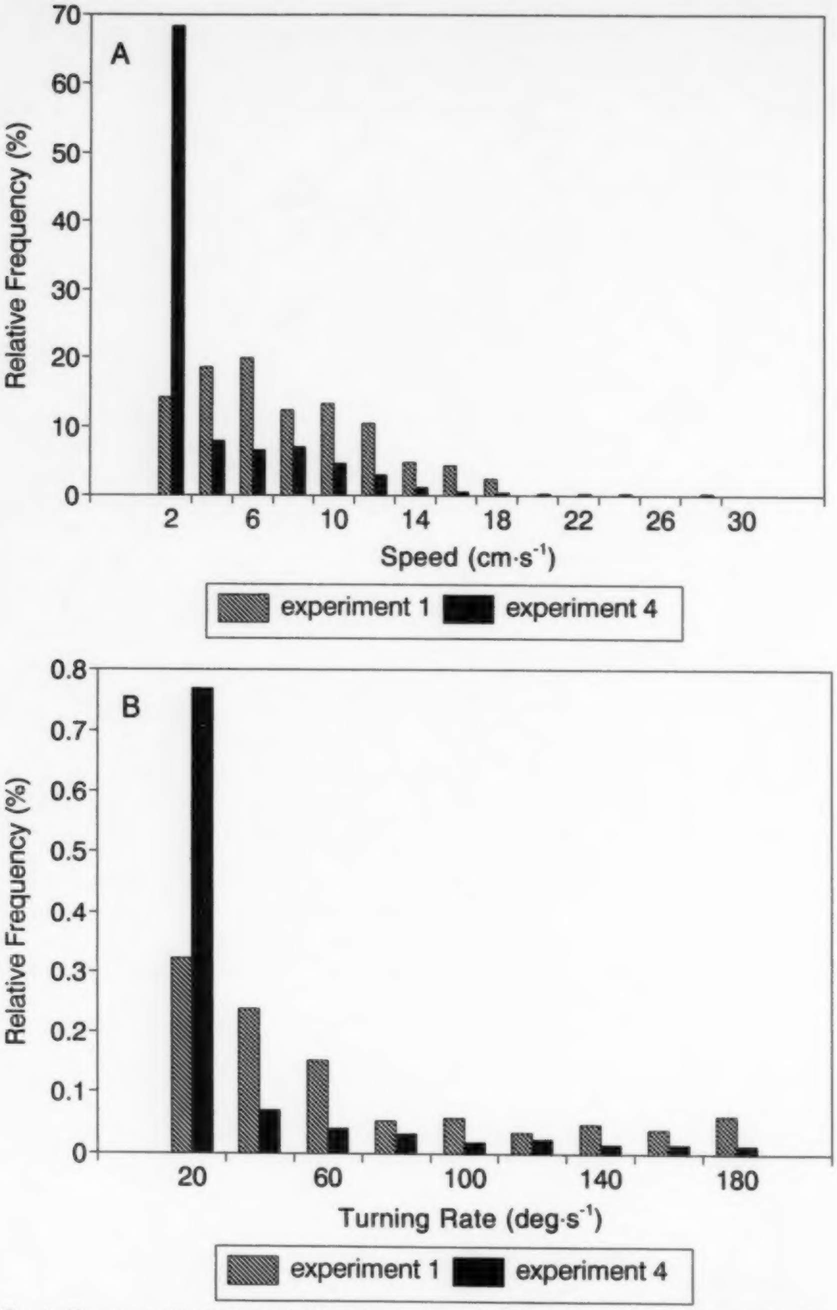

FIG. 1. Frequency distribution of (A) swimming speed, (B) turning ratio, and (C) acceleration for the two experiments with the highest and lowest averages to illustrate the range of swimming characteristics observed. (*Fig. 1 concluded next page*)

$$(5)\quad Q=\sum_{i=1}^{7}(|C_s - C_{si}|)$$

where C_s is the mean of the 7000 pseudo-spontaneous costs and C_{si} is the mean of the 1000 pseudo-spontaneous costs of group *i*. A frequency distribution was constructed from the 999 *Q* values obtained by random permutation along with the observed *Q* value from the original data. The position of the *Q* value estimated for our original data set relative to the frequency distribution of *Q* allowed us to determine the probability that the observed differences among experiments occurred by chance. The proportion of simulated values

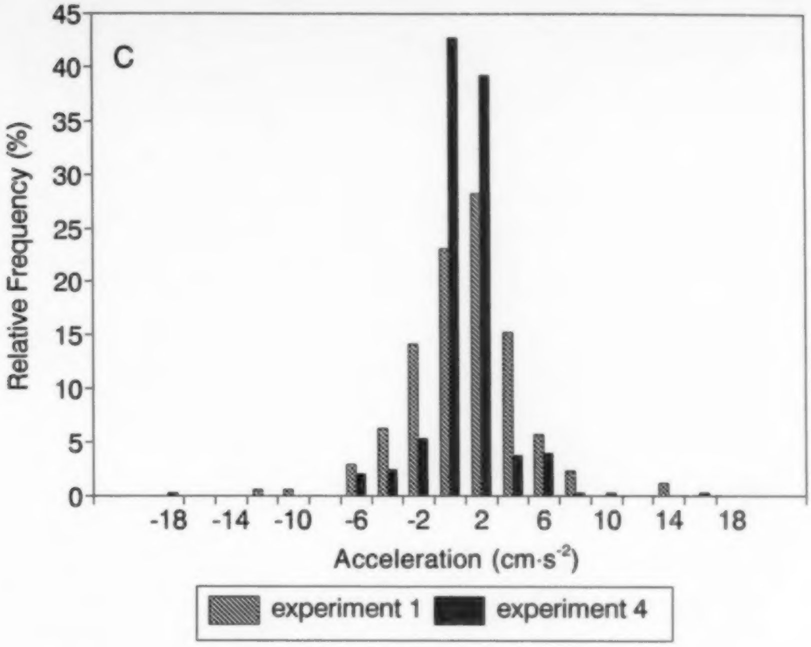

FIG. 1. (*Concluded*)

TABLE 2. Swimming characteristics and swimming cost ratios for spontaneously swimming fish in 28- to 108-L respirometers (n = sample size, $\bar{x}$ = average , 75% = 75th percentile, and CI = 95% confidence interval).

	Swimming speed (cm·s^{-1})			Turning rate (deg·s^{-1})			Acceleration (cm·s^{-2})			Swimming cost ratio	
Exp.	n	$\bar{x}$	75%	n	$\bar{x}$	75%	n	$\bar{x}$	75%	$\bar{x}$	CI
1	211	6.6	8.8	211	50	75	177	2.6	3.5	5.7	4.0–7.30
2	202	4.2	6.9	202	43	65	174	2.1	2.9	7.9	6.0–10.0
3	139	3.2	4.7	139	32	32	123	1.7	2.1	5.7	3.2–8.5
4	207	2.3	3.6	207	19	21	163	1.0	1.3	5.8	3.0–8.9
5	207	3.2	5.5	207	30	36	181	1.4	2.0	6.6	4.4–9.0
6	201	3.8	5.6	201	22	27	177	2.1	2.4	4.8	3.0–6.7
7	220	2.6	5.0	220	26	31	197	1.2	1.8	3.3	1.5–5.3

greater or equal to the observed statistic can be considered an approximate p-value for significant differences among experiments (Edgington 1987).

Swimming characteristics

The nonparametric (Kruskal–Wallis) one-way analysis of variance was used to compare average speed, turning rate, and acceleration among experiments. Absolute values of acceleration were used because the positive and negative accelerations would have cancelled out and resulted in average values always close to 0.

Forced swimming costs

The 95% CI associated with the average forced swimming cost for each experiment was obtained by creating a distribution of 1000 averages of 200 pseudo-speeds drawn at random (with replacement) from the 200 speeds obtained experimentally. Each pseudo-speed was converted to energetic cost using equation (3). The average cost for these 200 values was then multiplied by the proportion of time spent swimming. The 95% CI of average swimming cost for an experiment was defined as the 2.5th and 97.5th percentile of the 1000 averages.

Forced swimming costs among experiments were compared using the permutation procedure described for spontaneous swimming costs.

Swimming cost ratio

The 95% CI around the SCR estimates were obtained by creating a distribution of 1000 pseudo-SCR's. Each pseudo-SCR was the quotient of a pseudo-spontaneous swimming cost and a pseudo-forced swimming cost, both chosen randomly (with replacement) from the distribution of pseudo-values for the appropriate experiment. The resulting distributions were then compared using permutations as described for the spontaneous swimming costs.

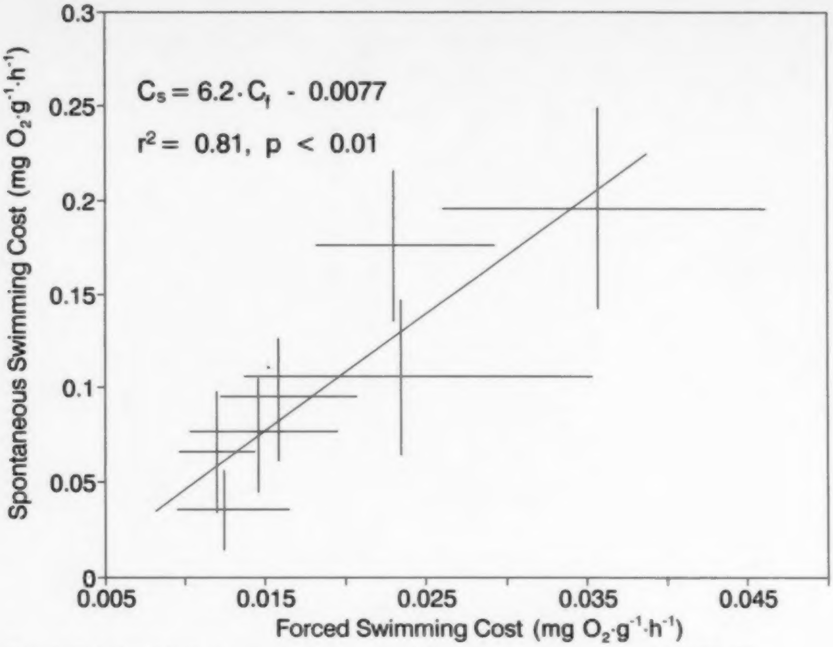

FIG. 2. Relationship between spontaneous and forced swimming costs with 95% CI.

Relationships between spontaneous swimming costs, forced swimming costs, swimming characteristics, and SCR

Regression analysis was used to examine relationships of spontaneous swimming costs as a function of forced swimming costs and swimming characteristics and SCR as a function of swimming characteristics. Although the distributions of speed, turning rate, and acceleration were skewed toward low values, the average was used rather than the median because we did not want to minimize the effect of rare but extreme values, as their importance in terms of energy consumption may be high (Brett and Groves 1979). We also used the 75th percentiles of the swimming characteristics as independent variables because they may represent the influence of rare but high-energy movements more appropriately than does the average.

Results

Spontaneous Swimming Costs

Routine metabolic rate (i.e., standard metabolism plus activity costs) ranged from 0.15 to 0.31 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ or 1.4–2.8 times the SMR. SMR interpolated from graphs in Job (1955) ranged from 0.11 to 0.13 mg $O_2 \cdot g^{-1} \cdot h^{-1}$. Spontaneous swimming costs differed significantly among experiments ($p < 0.001$) and varied from 0.04 to 0.20 mg $O_2 \cdot g^{-1} \cdot h^{-1}$.

Swimming characteristics

Average swimming speed varied significantly among experiments ($p < 0.0001$) and ranged from 2.3 to 6.6 $cm \cdot s^{-1}$ (Fig. 1A; Table 2). The 75th percentile varied 2.4-fold from 3.6 to 8.8 $cm \cdot s^{-1}$.

Turning rate was also significantly different among experiments ($p < 0.0001$). Average turning rate ranged from 19 to 50 $deg \cdot s^{-1}$. The 75th percentile for turning rate varied 3.6-fold from 21 to 75 $deg \cdot s^{-1}$ (Fig. 1B; Table 2).

Average acceleration varied significantly among experiments ($p < 0.005$) from 1.0 to 2.6 $cm \cdot s^{-2}$. The 75th percentile varied 2.7-fold and ranged from 1.3 to 3.5 $cm \cdot s^{-2}$ (Fig. 1C; Table 2).

Swimming speed, turning rate, and acceleration were consistently highest in Experiment 1 and lowest in Experiment 4 and exhibited roughly a threefold variation. The three swimming characteristics were highly intercorrelated. Pearson correlation coefficients between average speed and average turning rate, between average speed and acceleration, and between average turning rate and acceleration were 0.73 ($p < 0.05$), 0.86 ($p < 0.005$) and 0.66 ($p < 0.05$), respectively.

Forced Swimming Costs

The metabolic costs predicted using the forced swim model varied significantly among experiments ($p < 0.001$) and ranged from 0.012 to 0.036 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ (Fig. 2).

Prediction of Spontaneous Swimming Costs from Those of Forced Swimming

Eighty-one percent of the variability in spontaneous swimming costs was explained by forced swimming costs (Fig. 2). Because the y-intercept was not significantly different from 0 ($p > 0.79$), the slope indicates the factor by which the estimates based on forced swimming underestimate the actual, or spontaneous, cost of swimming. The slope was equal to 6.2 and was significantly different from 1 ($p < 0.05$).

Swimming Cost Ratio

The slope calculated above gives an index of the overall degree to which the forced swim model underestimates the spontaneous costs across the seven experiments. The SCR was calculated for each individual experiment as well to allow us to determine whether the SCR varied among experiments and, if so, whether the variability could be predicted with the swimming characteristics. SCR ranged from 3.3 to 7.9 (Table 2) and differed significantly among the seven experiments ($p < 0.001$). No significant relationship was found between SCR and swimming characteristics.

Prediction of Spontaneous Swimming Costs from Swimming Characteristics

Eighty percent of the variability in spontaneous swimming cost (C_s) was explained by average speed (S), 72% by average turning rate (T), and 80% by average acceleration (A) (Table 3). Using the 75th percentile for turning rate (TQ) improved the relationship between turning rate and spontaneous swimming cost ($r^2 = 0.83$). The 75th percentile for acceleration (AQ) explained only 3% more of the variation in spontaneous swimming cost than the average ($r^2 = 0.83$). The regression coefficient between swimming speed and spontaneous swimming costs was not affected by using the 75th percentile for speed (SQ). These relationships were also significant ($p < 0.05$) using the Kendall rank correlation (nonparametric) with the exception of the relationship between average turning rate and spontaneous swimming costs ($p > 0.10$). None of the intercepts was significantly different from 0 ($p > 0.25$).

The lack of independence among the swimming characteristics and the small number of experiments prevented us from developing a multiple regression model.

TABLE 3. Relationships between spontaneous swimming costs (C_s; mg $O_2 \cdot g^{-1} \cdot h^{-1}$) and forced swimming costs (C_f; mg $O_2 \cdot g^{-1} \cdot h^{-1}$) and between spontaneous swimming costs (C_s; mg $O_2 \cdot g^{-1} \cdot h^{-1}$) and mean speed ($S$; $cm \cdot s^{-1}$), 75th percentile of speed (SQ; $cm \cdot s^{-1}$), mean turning rate (T; $deg \cdot s^{-1}$), 75th percentile of turning rate (TQ; $deg \cdot s^{-1}$), mean acceleration (A; $cm \cdot s^{-2}$), and 75th percentile of acceleration (AQ; $cm \cdot s^{-2}$).

Model	r^2	f
$C_s = 6.2 \cdot C_f - 0.0077$	0.81	<0.01
$C_s = 0.036 \cdot S - 0.023$	0.80	<0.01
$C_s = 0.031 \cdot \mathrm{SQ} - 0.068$	0.80	<0.01
$C_s = 0.0045 \cdot T - 0.03$	0.72	<0.05
$C_s = 0.0026 \cdot \mathrm{TQ} + 0.005$	0.83	<0.005
$C_s = 0.095 \cdot A - 0.05$	0.80	<0.01
$C_s = 0.073 \cdot \mathrm{AQ} - 0.05$	0.83	<0.005

Discussion

Our results indicate that the costs associated with the activity of free-swimming fish are considerably larger than those predicted using relationships between metabolic cost and speed from forced swim respirometers (average of six times higher for our experiments) and that the magnitude of this difference can be variable (our range was 3.3- to 7.9-fold). Our results therefore support the theoretical (Webb 1991) and empirical (Boisclair and Tang 1993) indications in the literature that the metabolic costs of turning and acceleration may be substantial. Webb (1991), using hydrodynamic drag theory, estimated that the ratio of spontaneous to forced swimming costs (SCR) was approximately equal to 3, which is close to the low end of the range we found in our experiments. Boisclair and Tang (1993) modelled SCR as a function of fish weight and speed. For the range in fish weight and swimming speeds observed in our experiments, their model predicts an SCR between 10 and 15. The difference between the predicted range in SCR from Boisclair and Tang (1993) and the range we observed may be due to the more limited space available for swimming in the experiments used for their empirical model (four body lengths or less) than in our experiments where available space ranged from 3 to 12 body lengths. More complex swimming patterns due to space limitations in the experiments used for the empirical model may have led to the higher predicted swimming cost ratio than was found in this study. Forstner and Wieser (1990) examined patterns of routine swimming in juvenile roach using a respirometer–video system (Kaufmann 1983) designed to provide relative indexes of activity level in conjunction with measures of oxygen consumption. They also concluded that linear forward motion requires less energy than does more complex movement, although they did not quantify the differences observed.

Contrary to our expectations, among-experiment variability in SCR was not explained by swimming characteristics. The lack of a relationship may have been due to the large error associated with SCR estimates (SCR estimates incorporate error from both spontaneous and forced swimming costs), the limited range in swimming characteristics, and the small number of experiments.

Practical Implications

Although forced swimming costs did predict 81% of the variability in spontaneous swimming costs, they underestimated them substantially. The swimming characteristics explained a similar fraction of the variability in spontaneous swimming costs (up to 83%). It is our belief that relationships between the three swimming characteristics and spontaneous swimming costs have the potential to explain more of the variability in swimming costs than forced swimming costs which cannot account for any variability in turning rate and acceleration. Future research efforts should therefore be directed toward developing direct relationships between spontaneous swimming costs and swimming characteristics. In these particular experiments, swimming speed alone (and therefore, forced swimming costs) did not explain any less variation in spontaneous swimming than when turning rate and acceleration were included. These experiments, however, were characterized by a strong covariance among swimming characteristics. It was therefore not possible to quantify the relative influence of each swimming characteristic or to develop a multivariate model.

Calibrations designed to convert swimming characteristics observed in situ into metabolic costs must be developed in the laboratory, to allow for the measurement of oxygen consumption, but must also cover the range of swimming patterns observed in situ. The range of average turning rates observed in these seven experiments included the average turning rate observed in three in situ enclosures 1, 8, and 27 m^3 in volume (Tang and Boisclair 1993). Average swimming speed and acceleration, however, were lower in the experiments than in any of the three in situ enclosures. The enclosures are closer to natural conditions than are the respirometers because the fish are feeding, are at lower densities, and are less restrained in terms of space. To develop a model that can be used to convert in situ swimming characteristics into metabolic costs, experiments must be carried out in larger aquaria to allow the fish to reach greater speeds.

The difference between forced and spontaneous swimming costs is not only relevant for the calibration of the stereo-video method, but has also been recognized as being important for calibrating other methods for estimating activity rates such as location tracking (Webb 1991) and the telemetry of physiological correlates of activity such as axial muscle contractions (Weatherley et al. 1982; Kaseloo et al. 1992). Typically the costs associated with speeds obtained from location tracking are estimated from metabolic cost – forced swimming speed relationships and therefore do not account for costs associated with turning and acceleration.

The use of physiological correlates requires laboratory-determined relationships between oxygen consumption and signal frequency. Such calibrations can sometimes depend on swimming mode (Weatherley et al. 1982). When the unmonitored muscles are not used equivalently in the respirometer and in situ, the oxygen consumption associated with a given signal frequency in the laboratory may not adequately represent the energy expenditure associated with the same signal frequency in situ. Ideally, when developing the calibrations between signal frequency and oxygen consumption, the swimming patterns in the respirometer (and therefore the activity of unmonitored muscles) should represent in situ swimming patterns. Space limitations, however, are problematic with fish that must be large enough to carry transmitters.

Comparison with Other Methods

Of the few studies that have incorporated in situ estimates of activity rates into the fish energy budget, most have estimated swimming speeds from location tracking (Diana 1980; Stewart et al. 1983; Stewart and Ibarra 1991). It seems likely that location tracking underestimates activity costs both because the metabolic costs of turning and acceleration are not accounted for and because the low resolution for determining fish position leads to the underestimation of actual distance swum (Weatherley and Gill 1987). The advantages of the stereo-video method over location tracking are that it can account for costs associated with changes in direction and speed, has much greater resolution, and can determine fish position in three dimensions. Because the stereo-video method is not mobile and is limited by water clarity, the sampling volume is small and is not appropriate for recording large-scale movements of big fish recorded by location tracking. The stereo-video method and location tracking are potentially complementary because they record movements at different scales.

Promising results have been obtained with the telemetry of physiological correlates of activity such as heart rate and axial muscle contractions that can account for costs associated with local activity as well as long-range movements (Lucas et al. 1991; Kaseloo et al. 1992). However, telemetry is only appropriate for fish over 300 g because transmitter packages must be attached to or implanted in the fish.

No one approach is likely to be appropriate for all scales of activity and sizes of fish. There is presently a particular need for a method to estimate the in situ activity rates of small fish. Energy budgets developed for adult fish cannot be used to represent those of juveniles because weight-specific standard metabolism increases with decreasing size and young fish are characterized by both high activity and growth rates (Wieser and Medgyesy 1990; Shuter and Post 1990). Production of young fish and therefore their bioenergetic budgets is important from the point of view of examining recruitment and effects on both their predators and plankton community dynamics (Post 1990). The stereo-video method, by offering the potential for reliable in situ activity rates, can help us develop our understanding of the bioenergetic processes of young fish.

Acknowledgements

We thank Dr F.W.H. Beamish and T. Lyttle for their valuable and extensive assistance with respirometry techniques. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Quebec Ministry of Education (FCAR) through grants to the Freshwater Ecology Group of the University of Montreal, and the University of Montreal through CAFIR, Research Development Funds, and NSERC (Internal Funds).

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Littoral Fish Communities in Southern Quebec Lakes: Relationships with Limnological and Prey Resource Variables[1]

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Pierce, C.L., J.B. Rasmussen, and W.C. Leggett. 1994. Littoral fish communities in southern Quebec lakes: relationships with limnological and prey resource variables. Can. J. Fish. Aquat. Sci. 51: 1128–1138.

We assessed species richness, biomass, and community type of littoral fish in 10 southern Quebec lakes in relation to several limnological and prey resource variables. Lake, yearly, and seasonal variation in biomass was evaluated by quantitative, replicated seining. Species richness averaged 12.8 in our lakes, and 24 species were collected overall. Total littoral fish biomass averaged 13.5 g·m^{-2} overall and varied significantly among lakes (range 6.1–26.9 g·m^{-2}) and between early and late summer. Yellow perch (*Perca flavescens*), golden shiner (*Notemigonus crysoleucas*), and pumpkinseed (*Lepomis gibbosus*) occurred in all lakes and were the most abundant species overall, averaging 57% of the total fish biomass. Principal component ordination of littoral fish communities showed little evidence for aggregation of community types. Species richness was positively correlated with lake surface area ($r^2 = 0.62$), as has been shown in other studies. Total fish biomass was positively correlated with biomass of chironomids ($r^2 = 0.57$), which constituted 24% of the littoral invertebrate biomass in our lakes and are important prey of many fish species. We found no significant correlation between total fish biomass and total invertebrate biomass or between biomass of any of the dominant fish species and limnological or prey variables.

Nous avons évalué l'abondance des espèces, la biomasse et les types de communauté de poissons littoraux trouvés dans 10 lacs situés dans le sud du Québec en fonction de plusieurs variables limnologiques et ressources en proies. En procédant par sennage quantitatif et répété, nous avons évalué les variations saisonnières, annuelles et par lac de la biomasse. Nos lacs comptaient en moyenne 12,8 espèces et au total, 24 espèces ont été prélevées. La moyenne de la biomasse totale en poissons littoraux était globalement de 13,5 g·m^{-2}; la biomasse variait significativement d'un lac à l'autre (entre 6,1 et 26,9 g·m^{-2}) et entre deux périodes, soit le début et la fin de l'été. La perchaude (*Perca flavescens*), la chatte de l'est (*Notemigonus crysoleucas*) et le crapet soleil (*Lepomis gibbosus*) ont été trouvés dans tous les lacs; dans l'ensemble, c'étaient les espèces les plus abondantes, avec 57 % de la biomasse totale de poissons. Le classement par principales espèces des communautés de poissons littoraux n'a pas permis de mettre vraiment en évidence une aggrégation des types de communauté. Il existe une corrélation positive entre l'abondance des espèces et la superficie des lacs ($r^2 = 0,62$), comme on l'a établi ailleurs. Il existe aussi une corrélation positive entre la biomasse totale des poissons et la biomasse des chironomidés ($r^2 = 0,57$), qui correspondaient à 24 % de la biomasse des invertébrés littoraux dans nos lacs et qui sont aussi une proie importante pour de nombreuses espèces de poissons littoraux. Nous n'avons pas trouvé de corrélation significative entre la biomasse totale de poissons et la biomasse totale d'invertébrés non plus qu'entre la biomasse de toute espèce dominante donnée de poissons et les proies ou des variables limnologiques.

Received May 19, 1993
Accepted November 26, 1993
(JB940)

Reçu le 19 mai 1993
Accepté le 26 novembre 1993

Abundance and community composition of freshwater fishes have been topics of continued interest in fisheries ecology (Evans et al. 1987; Marshall and Ryan 1987; Wootton 1990). These communities have been examined using a number of different approaches, including intensive studies of a single or small number of systems (Wells 1977; Waters 1982; Lyons 1987, 1989; Elliott 1988; Johannes et al. 1989; Mills and Hurley 1990), comparative analyses of primarily literature data on biomass and fishery yields from many systems (Hanson and Leggett 1982; Kerr and Ryder 1988; Downing et al. 1990; Quiros 1990), and comparative analyses of fish species distributions from many systems (Rahel 1986; Jackson and Harvey 1989; Tonn et al. 1990; Hinch et al. 1991). Intensive studies frequently sample over an extended period of time, providing good estimates of temporal variability within the system. However, the range of variability encountered and the patterns of correlated responses among variables are difficult to extrapolate to other systems (Frost et al. 1988). Comparative analyses address spatial variation and patterns across many systems,

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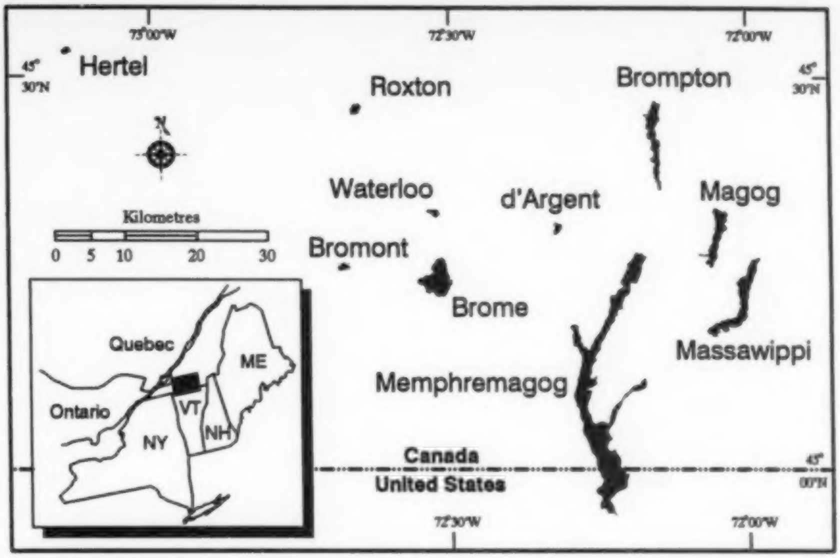

FIG. 1. Location of southern Quebec lakes sampled in this study. Lakes Bromont and Hertel are shown at twice actual size for clarity.

but often either ignore temporal variation by relying on single samples or assume temporal variation to be negligible by comparing samples or sample averages from different time periods. Few studies have examined spatial patterns of biomass and community composition across systems simultaneously with temporal variation (Hinch 1991), and we are aware of no such studies of littoral fish communities in lakes. Comparisons have been further hampered by the fact that many studies report only qualitative or relative abundances. Fewer still are studies that incorporate considerations for differences in gear efficiency and other sampling problems (Bayley 1985; Lyons 1987; Pierce et al. 1990).

The littoral zone fish fauna plays an important role in freshwater lake ecosystems (Northcote 1988). Abundance is typically greater than in other zones, and in many lakes, littoral species make up the bulk of the total fish community (Keast and Harker 1977; Werner et al. 1977). Littoral zone habitat and food resources are much more diverse than in other zones, potentially leading to complex relationships with the fish community. Intra- and interspecific interactions among littoral fishes are common, and the roles of predator, prey, and competitor undergo complex shifts in response to ontogeny, habitat, and resources (Mittelbach 1986). Littoral zone species are also frequently important as prey to larger, predominantly pelagic species (Lyons and Magnuson 1987). Characterization of patterns of biomass and community composition and development of empirical relations with limnological and prey resource variables should enhance our understanding of littoral fishes, just as similar efforts have yielded new insights with other components of aquatic systems (Peters 1986).

The purpose of this study was to assess the species richness, biomass, and community type of littoral zone fishes in 10 southern Quebec lakes in relation to several limnological and prey resource variables. Biomass was quantified using replicated littoral seining designed to evaluate both spatial (among-lake) as well as seasonal and yearly variation. Several limnological and prey resource variables were assessed concurrently with the fish sampling, and lake morphometric variables were obtained from the literature. We used principal components analysis to generate fish community, limnological, and prey community ordinations and explored relationships among these multivariate ordinations as well as bivariate relationships among individual variables.

Materials and Methods

Study Lakes

Our study was conducted in 10 lakes located in the Eastern Townships region of southern Quebec, Canada (Fig. 1). Several previous studies describe a variety of characteristics of these lakes, including pelagic zooplankton and phytoplankton (Pace 1984, 1986), littoral periphyton (Cattaneo 1987), sediments (Rowan et al. 1992), macrophytes (Chambers and Kalff 1985; Duarte and Kalff 1986; Anderson and Kalff 1988), benthos (Rasmussen 1988a, 1988b, 1993), growth of yellow perch (Boisclair and Leggett 1989a, 1989b, 1989c), and littoral fish sampling conditions (Pierce et al. 1990).

Estimating Fish Species Richness and Biomass

We sampled the littoral fish communities of each of the 10 lakes once in early summer and once in late summer during 1987 and 1988. The early summer period was from 18 June to 26 June in 1987 and from 4 July to 15 July in 1988. The late summer period was from 24 August to 17 September in 1987 and from 8 September to 22 September in 1988. Two replicate samples were taken in different locations at each lake during each sampling period. This sampling design allowed us to characterize the littoral fish communities and assess among-lake, yearly, and seasonal variation in biomass across the 10 lakes.

We used beach seines as described by Pierce et al. (1990) for all samples. In 1987, we used a 52 × 2.6 m knotless nylon (6-mm mesh) seine, with a continuous lead-core bot-

TABLE 1. Occurrence and mean biomass (untransformed) of fish species in the littoral zone of southern Quebec lakes. Species are listed in descending order of overall biomass. Numbers identifying lakes are given in Table 2.

Species	Common name	Lakes containing species	Mean biomass in lakes containing species ($g \cdot ha^{-1}$)
Perca flavescens	Yellow perch	All lakes	35 759
Notemigonus crysoleucas	Golden shiner	All lakes	22 293
Lepomis gibbosus	Pumpkinseed	All lakes	18 563
Moxostoma anisurum	Silver redhorse	7	86 296
Ameiurus nebulosus	Brown bullhead	All lakes	8 045
Catostomus commersoni	White sucker	All lakes	6 879
Esox lucius	Northern pike	1–7, 9, 10	7 590
Moxostoma valenciennesi	Greater redhorse	7	35 026
Esox niger	Chain pickerel	1–6, 8–10	2 693
Ambloplites rupestris	Rock bass	1, 3, 5–9	2 126
Fundulus diaphanus	Banded killifish	1–4, 8	1 852
Micropterus dolomieu	Smallmouth bass	1, 2, 4, 6–10	1 110
Hybognathus regius	Eastern silvery minnow	7	6 656
Semotilus corporalis	Fallfish	1, 3, 4, 7, 10	1 176
Pimephales notatus	Bluntnose minnow	1–4, 7–9	812
Notropis atherinoides	Emerald shiner	7, 8	2 583
Etheostoma nigrum	Johnny darter	1–3, 6–9	364
Luxilus cornutus	Common shiner	1, 2, 4, 8, 10	471
Micropterus salmoides	Largemouth bass	6, 8, 9	525
Semotilus atromaculatus	Creek chub	7, 10	541
Pomoxis nigromaculatus	Black crappie	9	675
Notropis hudsonius	Spottail shiner	2	270
Percina caprodes	Logperch	2, 7	81
Osmerus mordax	Rainbow smelt	6, 8	45

tom line, plastic floats along the top line, and a 2.6-m^3 bag in the center. In 1988, we used a seine of identical design but larger dimensions (100 × 3 m). The seine was deployed from a small boat in a semicircle extending out from the shoreline, enclosing an area of 430 m^2 in 1987 and 1600 m^2 in 1988. Depth at the deepest point of the enclosed area averaged 1.7 m. We pulled the seine to shore from both ends, with a diver and an assistant in the boat monitoring the progress of the seine. Captured fish were anesthetized immediately in 2-phenoxyethanol, put on ice, and frozen within a few hours. In the laboratory, fish were identified to species, measured (total length, TL) to the nearest millimetre, and weighed (wet) to the nearest 0.01 g. *Micropterus* and *Esox* species were measured (TL) immediately upon capture and released alive; wet weights for these species were estimated using equations in Carlander (1969) and Murphy et al. (1991). During the late summer sampling period in 1987 and both sampling periods in 1988, habitat and habitat-related variables such as macrophyte biomass, snags and seine rolling were quantified as described in Pierce et al. (1990).

We calculated biomass (wet grams per square metre) of individual species and the total fish community in each sample. Biomass estimates from the 1988 samples were corrected for variable capture efficiency using equations described in Pierce et al. (1990). The late summer samples from 1987 were corrected for capture efficiency using efficiency estimates obtained directly at the time of sampling. Efficiency estimates obtained from a given location tended to be similar, so we used the mean of all efficiency estimates from a given location as the correction for capture efficiency at that location in the 1987 early summer sampling period.

Estimating Limnological Conditions and Prey Resources

Water temperature, Secchi depth, chlorophyll *a* concentration, submerged littoral macrophyte biomass, and invertebrate prey biomass in each lake were sampled several times during the months of May–September in 1987 and 1988. Water temperatures were estimated using a combination of littoral and pelagic temperature profiles at 1-m depth intervals. Littoral temperature profiles were recorded near fish sampling areas from the surface to the bottom (approximately 3 m). Pelagic profiles were recorded at offshore locations from the surface to a depth of 3 m. Temperatures from individual profiles were averaged across depths, and these values were then averaged over the two years of sampling for each lake. Chlorophyll *a* concentrations were determined from integrated epilimnetic water samples obtained from offshore locations using a tube sampler; triplicate 500-mL subsamples were vacuum-filtered (65 μm) and frozen in the field and extracted in the laboratory (Strickland and Parsons 1972). Secchi depths were measured concurrently with water sampling. We sampled submerged littoral macrophyte biomass concurrently with fish samples as described in Pierce et al. (1990). Littoral sediment-dwelling and epiphytic macroinvertebrate prey were sampled as described in Rasmussen 1988a). Organisms were identified, counted, and measured for conversion to biomass using length–mass regressions (Smock 1980; C.W. Osenburg, Department of Integrative Biology, University of California, Berkeley, CA 94720, USA, unpublished data; J.B. Rasmussen, unpublished data). Littoral zooplankton prey were sampled at 07:00 by triplicate bottom-to-surface vertical hauls with a 30.5-cm-diameter, 75-μm-mesh net. Depths were recorded to the nearest 0.1 m and were generally near 3 m. A filtering efficiency of 46%, estimated by several calibrations with pooled Schindler–Patalas trap samples taken at 1-m intervals, was applied as a correction factor in biomass calculations. Samples were preserved in a sucrose–Formalin solution (Haney and Hall 1973). Organisms in subsamples (usually 10%) were identified and counted, and at least 30 individuals of each taxon were measured for conversion to biomass using length–mass regressions (Dumont et al. 1975; Culver et al. 1985).

Conductivity, surface area, mean depth, maximum depth, and water residence time data from each lake were obtained from published studies (Rasmussen 1988a; Rowan et al. 1992).

Statistical Analyses

Data were analyzed using analysis of variance (ANOVA), principal components analysis (PCA) ordination, correlation, and regression analysis. Lake, yearly, and seasonal variation in biomass of the total littoral fish community and dominant species was evaluated with three-way ANOVA, using $\log_{10}(x + 1)$ transformed data. We used three separate PCA ordinations to compare the 10 lakes on the basis of littoral fish communities, limnological conditions, and invertebrate prey communities. Lake averages of $\log_{10}(x + 1)$ transformed data were used as input variables for ordinations, and principal components were extracted from covariance matrices. For the fish community ordination, we used the eight species found in eight or more of the lakes, including yellow perch (*Perca flavescens*), golder shiner (*Notemigonus crysoleucas*), pumpkinseed (*Lepomis gibbosis*), brown bullhead (*Ameiurus nebulosus*), white sucker (*Catostomus commersoni*), northern pike (*Esox lucius*), chain pickerel (*Esox niger*), and smallmouth bass (*Micropterus dolomieu*). These eight species accounted for 75% of the littoral fish biomass estimated across all lakes. For the limnological ordination, we used chlorophyll *a*, Secchi depth, littoral macrophyte biomass, temperature, conductivity, surface area, mean depth, maximum depth, and water residence time. For the prey community ordination, we used biomass (wet grams per square metre) of chironomids, trichopterans, ephemeropterans, oligochaetes, gastropods, pelecypods, amphipods, and zooplankton. These groups accounted for over 95% of the littoral invertebrate biomass estimated across all lakes. Relationships of principal components between ordinations and of principal components with individual variables were explored using correlation analysis. Linear regressions were generated to describe relationships of littoral fish species richness and biomass with limnological and prey resource variables. All analyses were performed using the ANOVA, CORR, PRINCOMP, and REG procedures of SAS (SAS Institute Inc. 1988).

Results

Fish Species Richness

Twenty-four species were present in our samples (Table 1). All are considered native to this zoogeographic region, accounting for roughly 25% of the known species inhabiting the St. Lawrence River drainage (Underhill 1986). Overall species richness of individual lakes ranged from 8 to 17, averaging 12.8 (Table 2). Species richness of individual samples ranged from 2 to 12, averaging 7.6 across all sam-

TABLE 2. Littoral fish biomass and species richness, invertebrate prey biomass, and limnological characteristics in southern Quebec lakes. All data are untransformed; biomass data are wet mass.

Lake	Lake No.	Number of littoral fish species	Mean littoral fish biomass ($g \cdot m^{-2}$)	Mean littoral benthos biomass ($g \cdot m^{-2}$)	Mean littoral zooplankton biomass ($g \cdot m^{-2}$)	Mean littoral macrophyte biomass ($g \cdot m^{-2}$)	Mean chlorophyll *a* concentration ($\mu g \cdot L^{-1}$)	Mean Secchi depth (m)	Mean summer water temperature (°C)	Surface area (ha)	Mean depth (m)
Brompton	1	14	10.0	15.2	0.14	1896	2.39	4.0	21.0	1191	11.5
Brome	2	14	7.0	53.8	0.13	1101	6.74	3.2	20.1	1452	5.7
Bromont	3	12	11.4	63.4	0.91	3018	8.65	2.2	21.0	50	5.2
d'Argent	4	12	6.6	15.0	0.17	818	3.64	3.1	21.1	96	4.6
Hertel	5	8	10.7	43.3	0.14	1781	2.53	3.7	18.1	29	4.7
Magog	6	12	26.9	60.1	0.07	3302	5.46	2.8	18.5	1080	9.7
Massawippi	7	17	22.5	9.3	0.71	1773	2.70	3.6	17.5	1790	40.2
Memphremagog	8	15	6.1	38.6	0.20	2281	2.45	3.0	18.9	9010	19.8
Roxton Pond	9	13	16.0	29.5	0.46	1435	7.73	2.2	19.7	179	3.2
Waterloo	10	11	17.6	62.7	0.50	2408	21.54	0.9	21.0	150	2.9

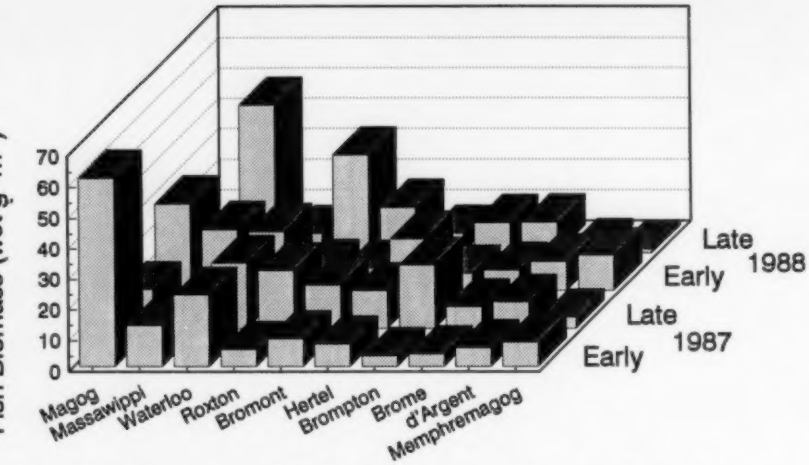

FIG. 2. Total fish biomass (untransformed) in the littoral zone of southern Quebec lakes during early and late summer of 1987 and 1988. Lakes are arranged in descending order of overall total biomass from left to right. Bars are means from two replicate samples.

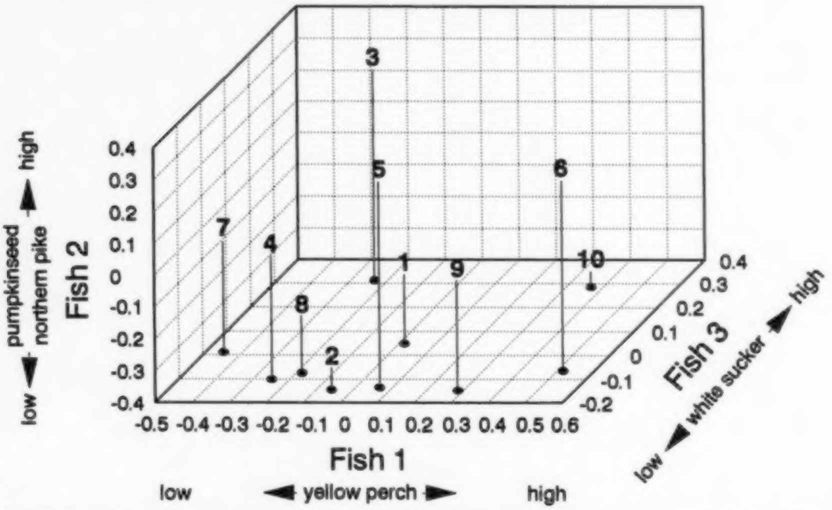

FIG. 3. Principal component ordination of littoral fish communities in southern Quebec lakes. Lakes are identified by numbers in Table 2.

ples. Individual samples contained an average of 61% of all species collected in their respective lakes over the course of the study. Five species (yellow perch, golder shiner, pumpkinseed, brown bullhead, and white sucker) were present in all 10 lakes. Three additional species were collected in at least eight of the 10 lakes. Five species were collected in only one lake.

Fish Biomass

Biomass of the total littoral fish community averaged 13.5 g·m^{-2} across all lakes. Mean total biomass varied more than fourfold among individual lakes, ranging from 6.1 to 26.9 g·m^{-2} (Table 2). Yellow perch, golden shiner, and pumpkinseed were the overall dominant species (Table 1), together accounting for 57% of the total fish biomass.

Total fish biomass varied significantly among lakes and between seasons, with the season of greatest biomass differing among lakes (Fig. 2; Table 3). Lakes Magog and Memphremagog had considerably greater littoral fish biomass in early summer than late summer whereas the pattern was reversed in Lakes Brompton, Bromont, and Roxton. Year effects were less pronounced than seasonal effects, with the exception of Lakes Magog and Massawippi. The three dominant littoral species showed the same general pattern of biomass across the 10 lakes: either strong lake × season interaction (yellow perch and golden shiner) or strong lake and season main effects (pumpkinseed) (Table 3).

Fish Community Ordination

PCA ordination of the littoral fish communities resulted in a general pattern of lakes scattered widely in principal component space, with little evidence of aggregation of com-

TABLE 3. Summary of ANOVAs testing the effects of lake (L), year (Y), and season (S) on biomass of total fish, yellow perch, golden shiner, and pumpkinseed in the littoral zone of southern Quebec lakes. Degrees of freedom for sources of variation are as follows: L, 9; Y, 1; S, 1; L × Y, 9; L × S, 9; Y × S, 1; L × Y × S, 9. Error mean squares for individual ANOVAs are as follows: total fish, 0.0382; yellow perch, 0.0288; golden shiner, 0.0646; pumpkinseed, 0.0321. Asterisks indicate significant effects: $*0.05 > P \geq 0.01$, $**0.01 > P \geq 0.001$, $***0.001 > P \geq 0.0001$, $****P < 0.0001$.

Group or species	Source of variation	*F*	*P*
Total fish	L	6.73	<0.0001****
	Y	0.11	0.746
	S	0.82	0.370
	L × Y	2.29	0.035*
	L × S	7.33	<0.0001****
	Y × S	4.95	0.032*
	L × Y × S	1.50	0.181
Yellow perch	L	20.42	<0.0001****
	Y	<0.01	0.990
	S	12.24	0.001**
	L × Y	3.07	0.007**
	L × S	6.18	<0.0001****
	Y × S	0.87	0.357
	L × Y × S	1.25	0.295
Golden shiner	L	4.54	0.0004***
	Y	4.44	0.041*
	S	2.47	0.124
	L × Y	2.09	0.054
	L × S	5.84	<0.0001****
	Y × S	0.08	0.773
	L × Y × S	1.14	0.356
Pumpkinseed	L	8.13	<0.0001****
	Y	<0.01	0.978
	S	13.53	0.0007***
	L × Y	1.23	0.305
	L × S	2.18	0.045*
	Y × S	0.06	0.808
	L × Y × S	1.78	0.102

TABLE 4. Correlations of fish species biomass with principal components from the PCA of littoral fish communities in southern Quebec lakes. *P* values are given in parentheses; % of variance explained is given at the bottom of the table.

	Principal component		
Species	Fish 1	Fish 2	Fish 3
Yellow perch	0.91 (0.0002)	−0.36 (0.308)	−0.05 (0.894)
Golden shiner	0.75 (0.013)	0.48 (0.158)	−0.15 (0.676)
Pumpkinseed	0.50 (0.143)	0.80 (0.006)	−0.05 (0.898)
Brown bullhead	0.56 (0.091)	−0.03 (0.932)	0.67 (0.033)
White sucker	0.05 (0.901)	0.04 (0.911)	0.98 (0.0001)
Northern pike	0.15 (0.687)	0.77 (0.009)	−0.04 (0.920)
Chain pickerel	0.42 (0.225)	0.26 (0.464)	0.14 (0.700)
Smallmouth bass	−0.56 (0.095)	−0.15 (0.671)	−0.04 (0.921)
% variance explained	46	25	14

munity types (Fig. 3). Communities in Lakes Bromont, Magog, and Waterloo appeared to be the most atypical among the 10 lakes. Principal component 1 (Fish 1) explained 46% of the variance and largely reflected biomass of yellow perch (Table 4), the most abundant species overall. Fish 1 was also positively correlated with biomass of golden shiner, the second most abundant species overall. Principal component 2 (Fish 2) explained 25% of the variance and reflected biomass of pumpkinseed, the third most abundant species overall, and northern pike. Principal component 3 (Fish 3) explained 14% of the variance and largely reflected biomass of white sucker. Fish 3 was also positively correlated with biomass of brown bullhead.

Limnological Conditions and Prey Resources

Mean limnological conditions and invertebrate prey biomass varied considerably among lakes, ranging from roughly fourfold variation in macrophyte biomass and Secchi depth to well over two orders of magnitude in surface area (Table 2). In contrast, mean summer water temperatures were fairly consistent among lakes, varying by only a few degrees.

Limnological and Prey Community Ordinations

PCA ordinations of the lakes based on limnological variables (Fig. 4a) and prey communities (Fig. 4b) revealed patterns broadly similar to the fish community ordination; lakes were widely scattered in principal component space and there was little evidence of aggregation. Principal component 1 (Limn 1) from the limnological ordination explained 76% of the variance and reflected lake size, correlating positively with surface area, mean depth, maximum depth, and water residence time (Table 5). Principal component 2 (Limn 2) explained 14% of the variation and appeared to reflect trophic conditions, correlating positively with chlorophyll *a*, macrophyte biomass, and conductivity and negatively with Secchi depth. The largest lakes in our data set tended toward intermediate trophic conditions (Fig. 4a).

Principal component 1 (Prey 1) from the prey community ordination (Fig. 4b) explained 40% of the variance and largely reflected biomass of molluscs, correlating positively with biomass of gastropods and pelecypods (Table 6). Molluscs accounted for over 50% of the littoral invertebrate prey biomass overall. Principal component 2 (Prey 2) explained 27% of the variance and reflected biomass of chironomids (Table 6), which accounted for 24% of the littoral invertebrate prey biomass overall.

Fish Community Relationships with Limnological Conditions and Prey Resources

The strongest relationships of fish communities with other lake characteristics were between fish species richness and measures of lake size (Fig. 5 and 6). Species richness was positively correlated with the principal component (Limn 1) expressing lake size (Fig. 5). Likewise, species richness was positively correlated with lake surface area and is shown

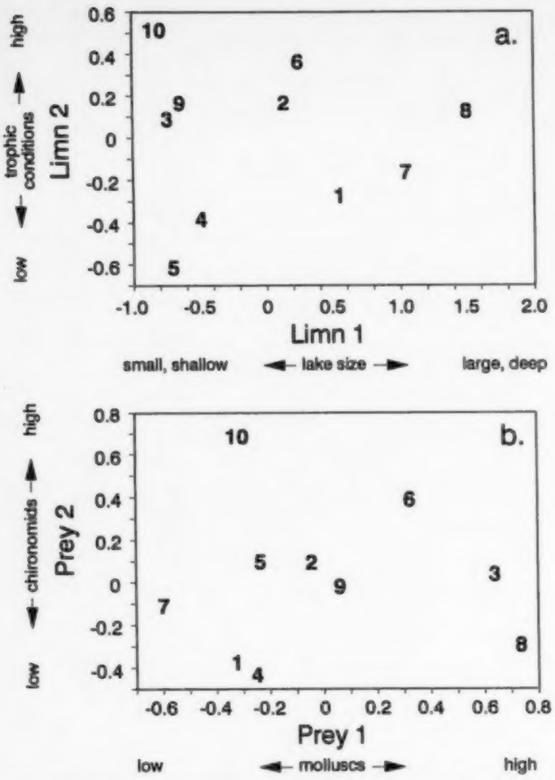

FIG. 4. Principal component ordinations of southern Quebec lakes based on (a) limnological variables and (b) invertebrate prey communities. Lakes are identified by numbers in Table 2.

in Fig. 6 plotted logarithmically to facilitate comparisons with two previous studies in Canadian lakes. Our species richness values compared well at the upper end of the lake size range, but were higher in smaller lakes than in previous studies. Species richness was also positively correlated with the other variables related to lake size: mean depth (r = 0.75, P = 0.013), maximum depth (r = 0.74, P = 0.015), and water residence time (r = 0.64, P = 0.044). No other significant correlations with species richness were seen.

We also found significant relationships of fish biomass with prey biomass. The principal component (Fish 1) expressing yellow perch and golden shiner biomass was positively correlated with the principal component (Prey 2) expressing chironomid biomass (Fig. 7), suggesting a relationship between the dominant community type and a major prey type. Total fish biomass was also positively correlated with Prey 2 (r = 0.69, P = 0.029) and, as expected from the very strong influence of chironomids on Prey 2 (Table 6), total fish biomass was positively correlated with chironomid biomass (Fig. 8). We found no significant correlation between total fish biomass and total invertebrate prey biomass (r = 0.01, P = 0.972). We then compared our data with Hanson and Leggett's (1982) empirical model of fish biomass based on the ratio of benthos biomass to mean depth (Fig. 9). As shown in Fig. 9, the correlation of total fish biomass with benthos·mean depth^{-1} as well as fit of our data to the model was poor.

TABLE 5. Correlations of limnological variables with principal components from the PCA of limnological data in southern Quebec lakes. P values are given in parentheses; % of variance explained is given at the bottom of the table.

Variable	Principal component Limn 1	 Limn 2
Chlorophyll *a*	−0.61 (0.059)	0.73 (0.016)
Secchi depth	0.52 (0.125)	−0.74 (0.015)
Macrophyte biomass	0.25 (0.479)	0.77 (0.009)
Summer water temperature	−0.48 (0.157)	0.20 (0.571)
Conductivity	0.24 (0.504)	0.67 (0.034)
Surface area	0.95 (0.0001)	0.23 (0.523)
Mean depth	0.91 (0.0003)	−0.15 (0.687)
Maximum depth	0.97 (0.0001)	−0.18 (0.624)
Water residence time	0.81 (0.004)	−0.24 (0.500)
% variance explained	76	14

TABLE 6. Correlations of invertebrate prey biomass with principal components from the PCA of prey community data in southern Quebec lakes. P values are given in parentheses; % of variance explained is given at the bottom of the table.

Taxon	Principal component Prey 1	 Prey 2
Chironomids	−0.02 (0.958)	0.95 (0.0001)
Trichopterans	0.39 (0.259)	0.09 (0.806)
Ephemeropterans	−0.18 (0.628)	−0.42 (0.231)
Oligochaetes	0.18 (0.610)	0.43 (0.217)
Gastropods	0.76 (0.011)	0.32 (0.375)
Pelecypods	0.93 (0.0001)	−0.20 (0.581)
Amphipods	0.64 (0.046)	0.17 (0.641)
Zooplankton	0.01 (0.981)	0.40 (0.247)
% variance explained	40	27

Discussion

Species richness in the 10 lakes we studied was roughly comparable with values from other studies in North American lakes at similar latitude (Schneider 1981; Tonn and Magnuson 1982; Eadie and Keast 1984; Rahel 1986; Matuszek and Beggs 1988; Jackson and Harvey 1989). Previous work in our 10 study lakes produced similar species lists, but fewer

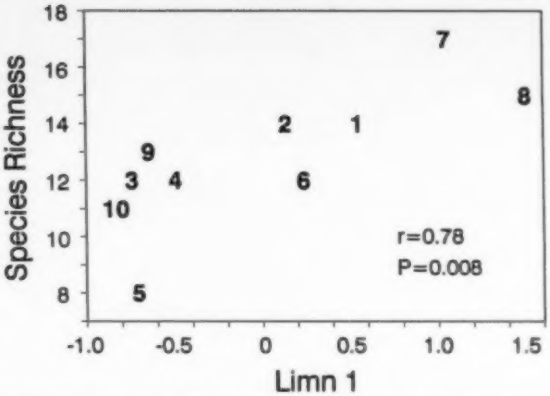

FIG. 5. Relationship of fish species richness in the littoral zone of southern Quebec lakes with scores from the first principal component (Limn 1) of the limnological ordination. Limn 1 represents variables related to lake size. Lakes are identified by numbers in Table 2.

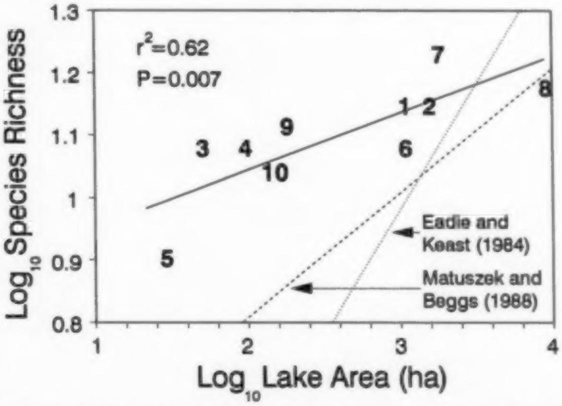

FIG. 6. Relationship of fish species richness in the littoral zone of southern Quebec lakes with lake surface area. The regression equation is $Y = 0.873 + 0.087X$; Y and X are $\log_{10}$ transformed values. Dotted and dashed lines represent relationships from previous studies for comparison. Lakes are identified by numbers in Table 2.

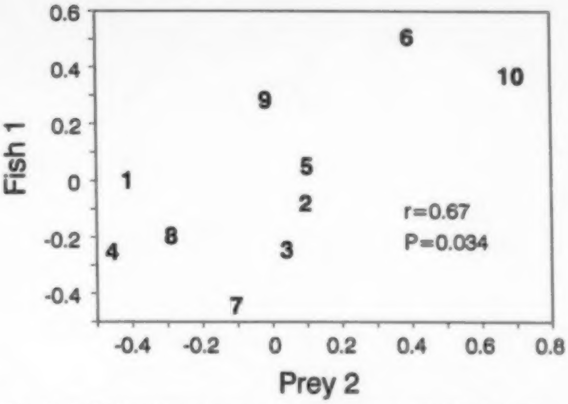

FIG. 7. Relationship of scores from the first principal component (Fish 1) of the fish community ordination with scores from the second principal component (Prey 2) of the prey community ordination in southern Quebec lakes. Fish 1 primarily represents abundance of yellow perch. Prey 2 primarily represents abundance of chironomids. Lakes are identified by numbers in Table 2.

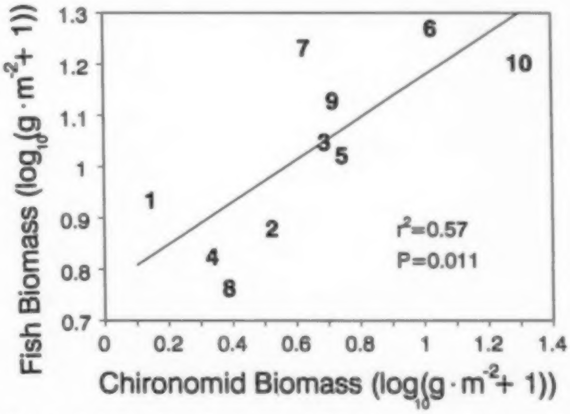

FIG. 8. Relationship of mean total fish biomass with mean chironomid biomass in the littoral zone of southern Quebec lakes. The regression equation is $Y = 0.770 + 0.404X$; Y and X are transformed as indicated. Lakes are identified by numbers in Table 2.

species were collected in all cases. Using similar sampling methods but half the number of samples (four), Boisclair and Leggett (1989c) reported species richness averaging 78% of our values. This percentage is roughly intermediate between our single-sample percentage (61%) and our total species richness (100%) values based on eight samples. This suggests that, despite coverage of large areas of the littoral zone in a single haul, numerous seine samples are necessary to detect the presence of rarer species. Provincial gillnet surveys (Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale de l'Estrie, 85 rue Holmes, Sherbrooke, QC J1E 1S1, Canada) also reported species richness averaging 78% of our values. Focusing on sport fish, their species lists included pelagic and offshore species (e.g., lake trout (*Salvelinus namaycush*), Atlantic salmon (*Salmo salar*), walleye (*Stizostedion vitreum*)) absent in our samples, but missed many of the smaller littoral species listed in Table 1. When compared with the combined species lists from all studies in the 10 lakes, our lists contained an average of 84% of the total species known to inhabit the respective lakes. Clearly, our intensive littoral sampling produced reasonably good estimates of species richness in these lakes. Large, deep lakes containing many offshore pelagic species require supplemental techniques.

Although the exact form of the relationship differed somewhat from previous studies (Fig. 6), our data confirmed the positive correlation of species richness with lake size described in previous work. Increased habitat diversity in larger lakes appears to be a likely causal factor producing this relationship (Eadie and Keast 1984; Matuszek and Beggs 1988). Our species richness values in larger lakes were very similar to those in lakes of comparable size from previous studies, but tended to be higher in smaller lakes (Fig. 6; see also fig. 5 in Jackson and Harvey 1989). These differ-

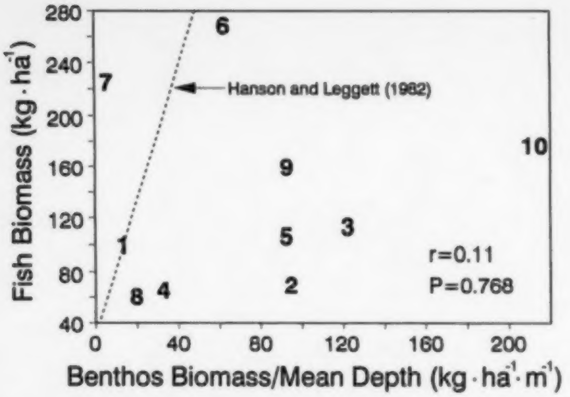

FIG. 9. Relationship of mean total fish biomass in the littoral zone of southern Quebec lakes with the ratio of mean benthos biomass to mean depth. The dashed line represents the relationship of Hanson and Leggett (1982) for comparison. Lakes are identified by numbers in Table 2.

ences may reflect differences in sampling methods; with the exception of the study by Eadie and Keast (1984), species richness data in other studies were obtained from a variety of sampling gears. Alternatively, differences in the form of the species richness – lake size relationship could be due to zoogeographical differences among study areas, as demonstrated by Jackson and Harvey (1989).

Our estimates of mean fish biomass in the 10 study lakes were well within the range of published values from several previous studies (Kempinger and Christenson 1978; Schneider 1978; Hanson and Leggett 1982; Downing et al. 1990). Hanson and Leggett (1982) compiled biomass data from the literature (most from cove rotenone studies in reservoirs) ranging from 0.3 to 86 $g \cdot m^{-2}$, with the majority of values falling between roughly 2 and 40 $g \cdot m^{-2}$. Downing et al. (1990) compiled a different data set from the literature with biomass values ranging from 0.5 to 37 $g \cdot m^{-2}$. Biomass estimates from 65 lakes in Michigan ranged from 1.1 to 40.3 $g \cdot m^{-2}$, averaging 13.1 $g \cdot m^{-2}$ (Schneider 1978). Our biomass range of 6.1–26.9 $g \cdot m^{-2}$, averaging 13.5 $g \cdot m^{-2}$, corresponded well with these literature values. The literature values outside our range could reflect a variety of factors, including reduced whole-lake biomass in comparison with our biomass data derived from the littoral zone, a wider range in lake productivity and other environmental variables, larger sample size, and differences in sampling efficiency.

To our knowledge, Boisclair and Leggett (1989c) have conducted the only previous quantitative fish sampling in our 10 study lakes. Using similar methods, but sampling only during one year and without making corrections for differential capture efficiency, they obtained biomass estimates that averaged 68% of our estimates. Our use of efficiency corrections probably accounts for some of this discrepancy. Although our average biomass estimates were higher than those of Boisclair and Leggett (1989c), we found a very similar pattern of relative biomass across the 10 lakes (r_s = 0.79, P = 0.006). This comparison suggests that, despite asynchronous temporal variation, our quantitative littoral seining did reveal a repeatable pattern in relative fish biomass among lakes.

Although significant interactions involving all three main effects occurred in our analyses of variation in fish biomass, lake and seasonal effects appeared to dominate (Fig. 2; Table 3). This further indicates that there were real differences in biomass among lakes, but also suggests that samples stratified over seasons were important for accurately estimating mean biomass in lakes. For example, had only the early season samples been taken, biomass estimates in Lakes Magog and Memphremagog would be considerably higher than our current values (Fig. 2). Likewise, biomass in Lakes Brompton, Bromont, and Roxton would be much lower than current estimates. The relatively weaker year effects suggest that stratifying sampling over more than one year might be less important than sampling seasonally within a single year if the primary goal is to make comparisons among lakes. However, the relatively short time scale of our study (2 yr) limits this interpretation. Long-term fluctuations in biomass are well known (Johannes et al. 1989; Lyons 1989; Townsend 1989; Mills and Hurley 1990) and should be addressed when possible.

PCA ordination of the lakes based on mean biomass of the eight most widely distributed species resulted in a general scattering of lakes, with little tendency toward aggregation, or "clumping", into similar community types (Fig. 3). Lakes Bromont and Waterloo were perhaps the most widely separated, both having high biomass of the benthic species white sucker and brown bullhead. Lake Magog was also somewhat separated from the other lakes, having the highest total biomass. The lack of distinct littoral fish community types in these lakes may have resulted for several reasons. Our study lakes were not widely separated geographically; the greatest distance between any two lakes is approximately 110 km (Fig. 1). Studies documenting distinct fish communities often cover larger spatial scales (Jackson and Harvey 1989; Tonn et al. 1990). None of our study lakes experience winterkill, low pH, or other severe forms of environmental stress that have been shown to produce distinct fish communities (Tonn and Magnuson 1982; Rahel and Magnuson 1983). Additionally, our use of quantitative biomass data rather than the more commonly used presence/absence data may have resulted in a more diffuse ordination of communities than in other studies.

Using relative abundance data, Hinch et al. (1991) have recently presented a similarly diffuse ordination of fish communities in a series of 25 central Ontario lakes. With a slightly different mix of dominant species, they found strong negative correlations in relative abundance of white sucker and rock bass (*Ambloplites rupestris*), and brown bullhead and smallmouth bass. White sucker were more numerous in lakes without piscivorous northern pike. These distributional patterns appeared to be primarily the result of differential habitat conditions, colonization histories, and possibly predation in the case of the northern pike/white sucker pattern. Our data suggested none of these relationships. Presumably, differences in environmental conditions, zoogeographic history, differences in sampling and analytical methodology, as well as the spatial scale of sampling account for these differences. Our southern Quebec lakes are in closer proximity and contained largely sympatric populations. The relationships described by Hinch et al. (1991) were the result of allopatric distributional patterns in the Ontario lakes and disappeared when only sympatric populations were considered.

Another potential explanation for the diffuse littoral fish community pattern could be the corresponding lack of aggregation of limnological and prey resource conditions among lakes (Fig. 4). Although these ordinations provided no basis for grouping the lakes into types, they did help identify some potentially important relationships of the littoral fish communities with environmental factors. Lake size, as described by principal component Limn 1, was positively correlated with species richness (Fig. 5), as discussed above. Lakes with chironomid-dominated littoral invertebrate prey communities (Prey 2) tended to have abundant yellow perch and golden shiner (Fish 1) (Fig. 7). This relationship suggested the positive correlation of chironomid biomass with total fish biomass (Fig. 8).

Empirical relationships of fish abundance, such as the one described above, have been very useful in generating testable hypotheses and providing working models for both management and further study in aquatic systems (Rigler 1982; Peters 1986, 1991). Existing models relate production, yield, or biomass to a variety of factors such as mean depth (Rawson 1952), morphoedaphic index (Ryder 1982), nutrient concentration (Hanson and Leggett 1982; Quiros 1990), primary productivity (Oglesby 1977; Downing et al. 1990), and benthos (Matuszek 1978; Hanson and Leggett 1982). In the majority of these models, predictor variables are considered to be generalized correlates of food availability, which is usually held to be the causal factor (Ney 1990), but is difficult to accurately assess (Boisclair and Leggett 1985). Our relationship of total fish biomass with chironomid biomass, which represented 24% of the overall littoral invertebrate biomass and the most abundant nonshelled group, may reflect such a causal relationship. Chironomids are widely known to be important in the diets of several fish species (Keast and Webb 1966; Sadzikowski and Wallace 1976). Previous work in our lakes indicated that chironomids were the only prey taxon to occur in the diets of all size classes of yellow perch examined and accounted for 27% of the diet (by weight) overall, the largest percentage of any prey taxon (Boisclair and Leggett 1989b). We are currently analyzing diets and consumption rates of the other two dominant species, golden shiner and pumpkinseed, in these lakes.

The lack of significant relationships of littoral fish biomass with measures of lake productivity and total benthos biomass may have several causes. Total measured prey biomass, or correlates such as productivity, may not reflect true availability of prey to fish (Boisclair and Leggett 1985). Differential vulnerability of prey taxa as well as food preferences among predators (Stein 1979; Zaret 1980; Peckarsky 1982; Pierce 1988) may complicate such relationships. Alternatively, responses of fish biomass in the littoral zone may be obscured by shoaling, offshore migrations, habitat heterogeneity, patchy distribution of prey, and other factors (Hall and Werner 1977; Keast and Harker 1977; Helfman 1978). Combining intensive littoral sampling such as ours with estimates of intrusion into nearby pelagic areas would be necessary to evaluate this possibility. An additional explanation might be that fish respond to environmental variation and food resource availability differently in different lakes, showing various combinations of growth, production, and biomass responses. Indeed, growth of yellow perch is highly variable among these lakes (Boisclair and Leggett 1989a, 1989b, 1989c), and preliminary data indicate similarly large differences in growth of golden shiner and pumpkinseed among the lakes (unpublished data). Clearly, relationships of littoral fish communities with the suite of limnological conditions, both biotic and abiotic, as well as the suite of prey resources available are necessarily complex. In addition to the analyses of community structure and biomass presented here, it is evident that evaluations of food resource utilization, growth, and production will be required to fully characterize links between the littoral fishes and their environment. We are currently exploring these relationships.

Acknowledgements

We thank Brian Walker, Lesley Pope, and Michel Simard for assistance in both the field and laboratory and Naga Kurra and Barb Thomas for assistance with compiling the data. Comments from Doug Austen, Peter Bayley, Marc Desjardins, and Dave Wahl improved the quality of this paper. Support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR), the Donner Foundation, and the Council for Faculty Research of Eastern Illinois University.

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Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) Utilization of Hawks Creek, a Small and Nonnatal Tributary of the Upper Fraser River[1]

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Scrivener, J.C., T.G. Brown, and B.C. Andersen. 1994. Juvenile chinook salmon (*Oncorhynchus tshawytscha*) utilization of Hawks Creek, a small and nonnatal tributary of the upper Fraser River. Can. J. Fish. Aquat. Sci. 51: 1139–1146.

Hawks Creek, a small tributary of the upper Fraser River where there is no record of spawning salmonids, was examined from May to November 1990 for the presence of juvenile salmonids. Age 0^+ wild chinook salmon (*Oncorhynchus tshawytscha*) appeared in May, increased to peak densities of 0.76 $\mathrm{fish{\cdot}m^{-2}}$ in late August, and were absent in November. Average residence time of marked chinook juveniles was 9 d. Duration of residency was size dependent, as small fish remained longer than large fish. Rainbow trout (*Oncorhynchus mykiss*) and mountain whitefish (*Prosopium williamsoni*) also had a short residency (mean = 21 d). We suggest that unsuitable rearing conditions (e.g., sediment load) in the mainstem Fraser River during the spring and summer favour the use of small, clear, and nonnatal tributaries by juvenile salmonids. Physical and biological explanations are proposed for their temporary use. These salmonid refuge habitats need to be protected.

De mai à novembre 1990, nous avons surveillé le ruisseau Hawks, un petit tributaire du Fraser dans sa partie amont, où on ne rapporte pas la présence de salmonides géniteurs, pour y trouver des salmonidés juvéniles. Des quinnats suivages d'âge 0^+ (*Oncorhynchus tshawytscha*) sont apparus en mai, ont atteint une densité maximale de 0,76 $\mathrm{poisson{\cdot}m^{-2}}$ à la fin août et étaient repartis en novembre. En moyenne, les quinnats juvéniles marqués restaient dans ce tributaire pendant 9 jours. La durée du séjour dépendait de la taille en ce sens que les plus petits poissons y demeuraient plus longtemps que les gros. La truite arc-en-ciel (*Oncorhynchus mykiss*) et le ménomini de montagnes (*Prosopium williamsoni*) séjournaient peu, eux aussi, dans ce cours d'eau (moyenne = 21 jours). Nous pensons que des conditions d'élevage défavorables (p. ex., charge en sédiments) dans le Fraser-même au printemps et à l'été poussent les salmonidés juvéniles à fréquenter les petits tributaires limpides qui ne sont pas leur lieu d'origine. Nous proposons des explications d'ordre physique et biologique à l'emploi temporaire de ces tributaires. Ces habitats qui servent de refuge aux salmonidés doivent être protégés.

Received February 19, 1993
Accepted December 8, 1993
(JB808)

Reçu le 19 février 1993
Accepté le 8 décembre 1993

Chinook salmon (*Oncorhynchus tshawytscha*) have highly variable life history strategies in freshwater. Some juveniles reside in or near their natal streams for a year after emerging from the streambed ("stream-type"; Healey 1983). Other juveniles reside in their natal streams for only a few days or months after emergence before migrating to the ocean ("ocean-type"). Both strategies are observed among most populations of chinook salmon from the Fraser River, British Columbia, but stream-type behaviour is more prevalent in the upper tributaries (Tutty and Yole 1978), while ocean-type behaviour is more prevalent in the lower tributaries (Levy 1984; Murray and Rosenau 1989).

Chinook salmon from the upper watershed of the Fraser River migrate long distances to the ocean, often spending months in freshwater, a form of stream-type behaviour. Juveniles from the Nechako (Russell et al. 1983), McGregor (Tutty 1979), Bowron (Murray et al. 1981), and Quesnel (Whelen et al. 1981) River populations travel 675–930 km to the ocean. They feed along the margins of the Fraser River during both summer (Levings et al. 1985) and winter months (Levings and Lauzier 1991).

During their migration, chinook juveniles have been observed using upper Fraser tributaries in which there is no record of spawning adults. Fry that were marked in the Nechako (Russell et al. 1983) and Chilcotin rivers (Delaney et al. 1982) were recovered in smaller downstream tributaries. They have reared in Nechako tributaries throughout the summer and early autumn (Russell et al. 1983). Small Fraser tributaries such as Stoner (Stone) and Hawks Creek also contained juvenile chinook salmon during the summer. Three hundred and ninety-six juveniles were caught in Hawks Creek during August 1984, but only two fish were caught during late October (Levings et al. 1985).

Chinook fry used nonnatal streams of the lower Fraser Valley for ~10 wk (Murray and Rosenau 1989). These fry appeared to exhibit ocean-type behaviour because none were caught after June 30. They probably originated from the Harrison River being displaced downstream, as 25% of Fraser chinook salmon originate from this river (Murray and Rosenau 1989). The rearing of juvenile chinook salmon in nonnatal streams appears common throughout the Fraser watershed.

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[1] Contribution No. 5 of the Fraser River Sustainable Development Program.

The physical environment in small nonnatal tributaries is different than that of the Fraser River. Peak flows and sediment loads during spring snowmelt occur much earlier in these tributaries than in the Fraser River (Anonymous 1973–90) because their elevations and latitudes are lower than the portion of the Fraser watershed above their confluences. Tributary temperatures and flows are more variable than those of the Fraser River because tributary watersheds are small and subject to local meteorological conditions.

When, why, and how long juvenile chinook salmon use nonnatal streams of the upper Fraser basin is poorly understood. We determined when and for how long juvenile chinook salmon used Hawks Creek during 1990. The importance of this habitat to salmonids and the physical and biological factors controlling its use were also examined.

Methods

Hawks Creek is a small stream (~20 km^2 watershed) that flows into the east side of the Fraser River near Soda Creek, B.C. (22 km north of Williams Lake). Salmon are not known to spawn in Hawks Creek (Manzon and Marshall 1980) and a barrier to upstream fish migration exists 300 m upstream from its confluence with the Fraser River. This 300-m-long reach from confluence to barrier was the study area. The reach has <2% gradient and is shaded by a poplar, birch, and willow layer of trees 1–3 m in height and by pine trees 15–25 m in height. Riffle/pool sequences occur at ~10-m intervals along its length. During the summer, water from Hawks Creek is used to irrigate hay fields located above the fish barrier.

In 1990 and 1991, winter flows were low and snow and ice built to a height of 3 m at the confluence of Hawks Creek and the Fraser River. In April, peak stream flows and sediment loads breached the ice when the snow melted in Hawks Creek watershed (water level = 1.2 m and sediment concentration = 689 mg·L^{-1} on April 16, 1991). Hawks Creek was clear by May, when flows and sediment loads in the Fraser River were still increasing (Carson 1988). Water levels and sediment concentrations in Hawks Creek increased for a few days during May–June rain storms as was observed on June 29, 1990.

The number and distribution of fish in our study reach were determined on 12 occasions between May 18 and November 1, 1990. Fish were collected with a 3.5-m-pole-seine, identified to species, counted, and then released. Each riffle/pool area was measured once the area fished was measured on each sampling date. All fishable areas (27–42% of total wetted area) were seined so that fish distribution in the study reach could be determined. After June 29, all captured salmonids were anaesthetized in 2-phenoxyethanol, checked for marks, marked with a cold brand, and measured for fork length (FL). A branding iron was cooled to −60°C in dry ice and acetone and then shaken dry before each fish was marked (Brown 1985). A different mark was used for each sampling date. The age of captured fish was determined from FL distributions and from scales removed from selected fish >100 mm FL. When loss of marks through emigration was not significant or when it could be calculated, population size was estimated when the formula $N = r(n + 1)/(m + 1)$ where N was the estimate of population size, r was the number of marks at risk, n was the number captured, and m was the number of marks recovered (Begon 1979).

Stream temperature and water level were determined for Hawks Creek and the Fraser River on 14 occasions between May 18, 1990, and April 23, 1991. On both the Fraser River and Hawks Creek, a water quality station was established ~100 m upstream of their confluence. Stream temperature was measured to the nearest 0.2°C with a hand-held thermometer at both stations. In Hawks Creek, water level was measured to the nearest 3 mm with a staff gauge. Water levels and flows of the Fraser River were available for the Marguerite ferry site, ~30 km upstream (Anonymous 1973–90).

A pair of suspended sediment samples were collected at both stations on 13 occasions between May 27, 1990, and April 23, 1991. They were obtained from the Hawks Creek station either with a DH48 depth integration sampler or at the point of greatest turbulence in the stream. Fraser River samples were collected 5 m from the water's edge in less turbulent water than Hawks Creek. A measured volume of each sample was passed through a preweighed filter which was then dried and reweighed. Suspended sediment concentrations were calculated as the mean of the paired samples in milligrams per litre.

Sediment concentrations from the Fraser River margin near Hawks Creek were compared with mean values from Marguerite and with values reported in the literature. Mean daily concentrations of suspended sediment were available for 1971–86 from the channel cross-section at Marguerite (Carson 1988), but data were fragmentary for 1990 (B. Tassone, Inland Waters Directorate, DOE, North Vancouver, B.C., personal communication). Where possible, sediment concentrations (milligrams per litre) reported in the literature were converted to nephelometric turbidity units (NTU) using conversion equations specific to the reported sediment type (Noggle 1978; Sigler et al. 1984; Lloyd et al. 1987). The equivalent concentration of Fraser River sediment was calculated from $\mathrm{NTU} = 0.188{\cdot}[\mathrm{mg{\cdot}L^{-1}}]^{0.916}$ (Servizi and Martens 1992).Thus, their reported values and results were comparable with our own.

Results

Abundance and area occupied by juvenile chinook salmon increased during the spring and decreased during the autumn in the Hawks Creek study reach. Few fish were caught on May 18, but the abundance of age 0$^+$ juveniles increased during May and June, declined in July after the June 29–30 storm, increased again in August, and declined again during September and October (Table 1). Juvenile chinook salmon were confined to the lower half of the study reach during May, but they were distributed throughout most of it during the summer. The area occupied increased, while total catch showed little variation between May 27 and July 6 (Table 1). The few fish that remained during October and November were confined to the top and bottom of the study reach.

Chinook salmon use of Hawks Creek was limited almost exclusively to age 0$^+$ fish from wild stocks. A single age 1$^+$ fish was caught near the mouth on May 27 (Table 1). Hatchery chinook salmon did not appear to use Hawks Creek, as juveniles with marked adipose fins were never captured. During the spring of 1990, 579 000 chinook juveniles were

TABLE 1. Numbers, FL range or mean (SE in parentheses), areas fished, catch per unit effort, and areas with fish (%) for juvenile chinook salmon caught in the Hawks Creek study reach during 1990. Numbers and sizes are also shown for rainbow trout and mountain whitefish. Size ranges were estimated prior to July 6 because all fish were not anaesthetized and measured.

	Chinook salmon					Rainbow trout		Mountain whitefish	
Date	Number	mm (FL)	Area seined (m^2)	Number·m^{-2} seined	% of area occupied	Number	mm FL	Number	mm FL
May 18	3	<50	137	0.02	26	6	~80–300	3	
27	66	~50–100	164	0.40	56	5	~80–220	5	
June 29	63	~50–60	77	0.82	91	1	~100	21	~48–200
July 6	69	61.3 (0.34)	151	0.46	94	2	115, 118	5	48–133
12	61	60.3 (0.33)	166	0.37	73	1	120	5	49–145
Aug. 22	140	70.4 (0.23)	140	1.00	81	6	100–203	17	53–191
25	149	69.1 (0.25)	145	1.03	92	6	111–250	4	77–86
Sept. 8	86	72.7 (0.31)	158	0.55	83	2	159, 162	12	80–185
13	46	73.4 (0.43)	137	0.33	74	1	159	2	88, 136
30	32	78.0 (0.48)	164	0.20	62	2	135, 160	1	75
Oct. 7	12	74.7 (0.74)	145	0.08	50	3	115–235	0	
Nov. 1	2	72, 81	102	0.02	8	0		0	
Total =	729					35		74	

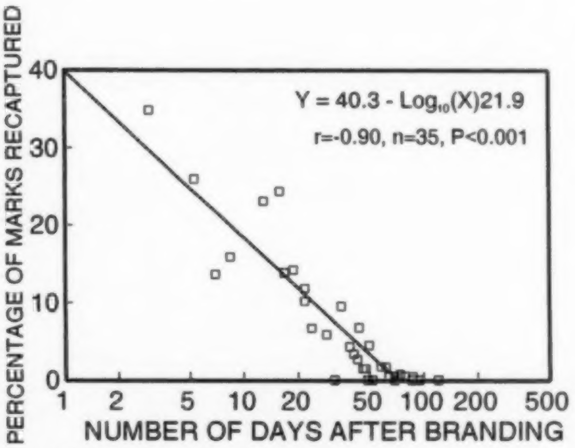

FIG. 1. Relationship between the percentage recovery of marked juvenile chinook salmon and the number of days since the mark was applied in Hawks Creek.

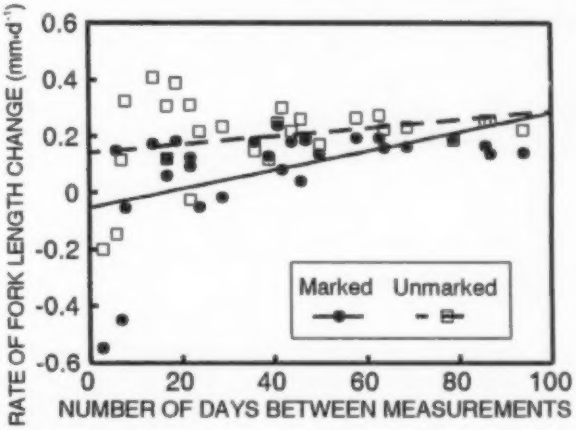

FIG. 2. Comparison of the rate of change in mean FL for branded chinook salmon ($r = 0.49$, $n = 28$, $P < 0.01$) with the rate of change in mean FL for unmarked fish ($r = 0.28$, $n = 28$, $P = 0.15$) in Hawks Creek.

released from up river hatcheries and 550 000 of them had been marked by removal of their adipose fins.

Average residence time in Hawks Creek was 9 d for individual chinook salmon (Fig. 1). The percentage recovery of brands was inversely correlated with the number of days since the mark was applied. Recaptures were rare after 55 d. The 140 chinook salmon that were branded on August 22 (Table 1) represented 40.3% (1 d; Fig. 1) of the Hawks Creek population on that date. By August 25, emigration had caused a decline of marks to 29.9% of the population ($40.3 - (\log_{10}3.0 \cdot 21.9)$; Fig. 1), or 104 fish ($140 \cdot 29.9/40.3$).

Residence time was size dependent for juvenile chinook salmon in Hawks Creek. Average daily rate of increase in mean FL was correlated with the number of days between sampling dates ($r = 0.37$, $n = 56$, $P < 0.01$), but the relationship was different for marked and unmarked fish ($F = 5.41$, df = 2,52, $P < 0.01$). The rate of change in size was positive for unmarked fish, while it was smaller, frequently negative, and more dependent on time for marked fish (Fig. 2). Since there were such large differences in rates of size change between marked and unmarked fish and the possibility of negative growth was unlikely, we concluded that large fish were leaving the marked population faster than small fish.

Maximum population size in the study reach could be estimated with mark–recapture data from August 22 and 25. The chinook population peaked between 346 ± 107 on August 22 (Fig. 1) and 325 ± 67 on August 25. Thus, average peak density was 0.76 fish·m^{-2} for 443 m^2 of stream and 2.36 fish·m^{-2} for the area fished (Table 1).

The size of juvenile chinook salmon increased throughout the summer in Hawks Creek (Table 1). Mean FLs of 60, 70, and 78 mm were achieved by early July, late August, and September 30, respectively.

Rainbow trout (*Oncorhynchus mykiss*) and mountain whitefish (*Prosopium williamsoni*) were also caught, in low num-

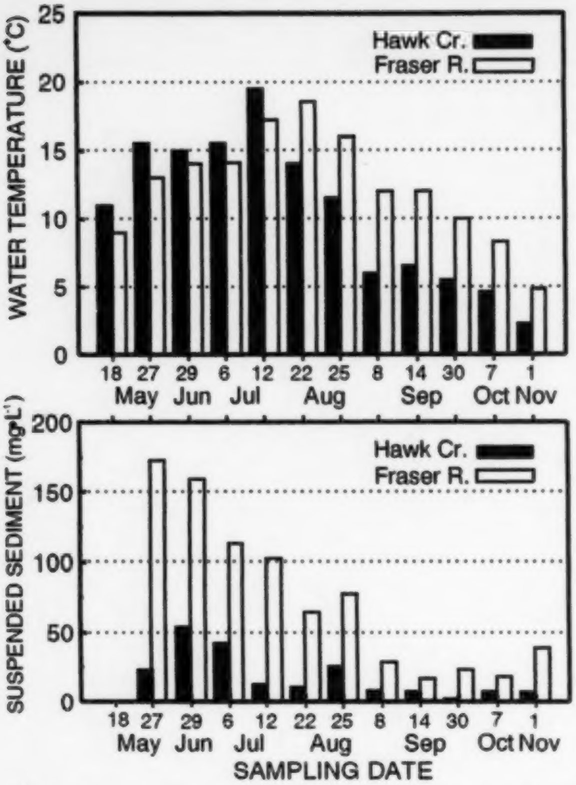

FIG. 3. Steam temperatures and suspended sediment concentrations in Hawks Creek and the Fraser River at Soda Creek, B.C., during May–November 1990.

bers, throughout Hawks Creek (Table 1). Mountain whitefish were caught on every spring and summer sampling date, but they were rare after September 8. They were distributed throughout the study reach. Size ranges and scales indicated that mountain whitefish and rainbow trout were represented by two or three age classes on most sampling dates (Table 1). They had short residence times, as few brands were ever recovered. Only three (13%) of the 23 marked rainbow were recaptured within 3, 39, and 43 d of marking. Four (9%) of the 46 branded whitefish were recaptured within 14–19 d of branding.

Concentrations of suspended sediment in Hawks Creek were lower than those of the Fraser River. In Hawks Creek, concentrations were <25 $mg{\cdot}L^{-1}$ from May to November except as a consequence of the June 29–30 rain storm (Fig. 3). A peak of 689 $mg{\cdot}L^{-1}$ occurred during snowmelt in April (April 16, 1991). Along the margin of the Fraser River, sediment concentrations were >150 $mg{\cdot}L^{-1}$ during May and June and exceeded 60 $mg{\cdot}L^{-1}$ throughout the summer (Fig. 3). At the Marguerite site, mean concentration was 435, 656 (peak) and 86 $mg{\cdot}L^{-1}$ on April 27, June 3, and August 15, 1990, respectively.

Water temperatures and water levels in Hawks Creek were also different from those of the Fraser River. Hawks Creek was >2°C warmer during May, June, and July and >5°C cooler during August and September than the Fraser River (Fig. 3). During October and November, stream temperature declined to <5°C in Hawks Creek. Water level in Hawks Creek declined throughout the summer except during the June 29–30 rain storm. By late August, the stream consisted of a series of pools that were connected by narrow (0.5 m) and shallow (~10 cm) riffles. Water level in the Fraser River declined continuously after July 15.

Discussion

Salmonid use of Hawks Creek is possibly controlled by a combination of physical and biological factors. Low water levels limited access, and cold temperatures and poor cover probably reduced suitability of the habitat from November to April. Age 0^{+} chinook salmon started emigrating from their upstream natal tributaries in mid-April, peak emigration occurred during mid-May, and emigration ended by late June (Tutty 1979; Murray et al. 1981; Whelen et al. 1981; Russell et al. 1983). They probably migrated down the margins of the Fraser River seeking the lower sediment concentrations and velocities. We suggest that during May–August, salmonids were attracted to the clearer and warmer waters of Hawks Creek. The high densities and changes in fish habitat preferences might have caused them to remain only a short time. Some fish also returned to the Fraser River when local rains on June 29–30 increased Hawks Creek flow and sediment levels. During September and October, declining water levels, velocities, and temperatures in Hawks Creek and declining sediment concentrations in the Fraser River might have reduced the need for and access to this refuge habitat. All ocean-type chinook salmon have passed Hawks Creek by autumn, while those showing stream-type behaviour either remained in their natal tributaries until next spring (Tutty and Yole 1978; Delaney et al. 1982) or clustered along the margins of the Fraser River for the winter (Levings and Lauzier 1991).

During late spring and early summer, juvenile chinook salmon used the margins of large rivers, probably because sediment concentrations and water velocities were much lower there than in the thalweg. Along the margins of the Fraser River, sediment concentrations ranged from 26% (spring peak) to 70% (mid-August) of mean values (Tywoniuk and Cashman 1973; Carson 1988). Chinook salmon of 50–70 mm FL also preferred velocities of ~20 $cm{\cdot}s^{-1}$ along the margins of Idaho (Hillman et al. 1987) and British Columbia rivers (Nechako River Project 1987). During late spring and early summer, these velocities in the Fraser River were only encountered along the margins (Anonymous 1973–90).

During spring and early summer, we believe that stress from high sediment in the Fraser River could have induced juvenile salmonids to move temporarily into Hawks Creek in order to feed and to clear their gills of sediment. Juvenile chinook salmon captured in Hawks Creek during August 1984 had many chironomids in their stomachs (Levings et al. 1985) and their foraging rates are known to decline when Fraser River sediments exceed 200 $mg{\cdot}L^{-1}$ (Gregory 1990). Juvenile salmonids become acclimated or attracted to the equivalent of Fraser River sediment of 20–40 $mg{\cdot}L^{-1}$ (Chapman and Bjornn 1969; Bisson and Bilby 1982), but concentrations of 50–99 $mg{\cdot}L^{-1}$ reduced feeding efficiency among coho salmon (*Oncorhynchus kisutch*; 11 NTU converted from Berg and Northcote (1985) and angler catch of other salmonids (≤99 $mg{\cdot}L^{-1}$; Lloyd et al. 1987). Exposure

TABLE 2. Summary of concentrations in equivalents of Fraser River sediment that result in 50% lethal responses within 96 h (96-h LC_{50}) among juvenile salmonids. Sources of data and relative sensitivity with Arctic grayling are also shown.

Species	Lethal concentration ($mg \cdot L^{-1}$)	Relative sensitivity with Arctic grayling	Source
Arctic grayling	100 000	1×	McLeay et al. 1987
Chum salmon	55 000	1.8×	Smith 1978
Rainbow trout	49 000	2.0×	Lawrence and Scherer 1974
Chinook salmon	31 000	3.2×	Servizi and Gordon 1990
Coho salmon	22 700	4.4×	Servizi and Martens 1991
Lake whitefish	17 700	5.6×	Lawrence and Scherer 1974
Sockeye salmon	17 600	5.7×	Servizi and Martens 1987

to the Fraser River sediment equivalent of 100–155 $mg \cdot L^{-1}$ caused reduced growth rates and some downstream displacement among steelhead and coho salmon (Sigler et al. 1984) and among some trout (Lloyd 1987). Chronic exposure to sediment of ~195 $mg \cdot L^{-1}$ caused consistent downstream displacement of juvenile steelhead and coho salmon (Sigler et al. 1984), increased susceptibility to fin rot among rainbow trout (Herbert and Merkens 1961), impaired feeding and growth among arctic grayling (*Thymallus arcticus*; McLeay et al. 1987), and increased activity among lake whitefish (*Coregonus clupeaformis*; Lawrence and Scherer 1974). Suspended sediments of 220–300 $mg \cdot L^{-1}$ caused elevated levels of blood sugar, an eightfold increase in cough rates, surfacing in the water column, and fright behaviour among young coho salmon (Bisson and Bilby 1982; Servizi 1990; Servizi and Martens 1992) and downstream displacement and reduced tolerance to pulp mill pentachlorophenols among arctic grayling (McLeay et al. 1987). Suspended sediments of 450–600 $mg \cdot L^{-1}$ caused extreme stress to juvenile coho salmon which was demonstrated by the cessation of feeding (Noggle 1978), reduced resistance to pathogens (Neitzel et al. 1985), elevated levels of plasma cortisol (Redding et al. 1987), and distinct avoidance even among salmonids acclimated to turbid waters (Bisson and Bilby 1982). Adult chinook salmon have avoided sediment concentrations of 350 $mg \cdot L^{-1}$ (Brannon et al. 1981) and 650 $mg \cdot L^{-1}$ (Whitman et al. 1982), but the literature contains little information about juvenile responses.

The stress levels of Fraser River sediment on juvenile chinook salmon, mountain whitefish, and rainbow trout near Hawks Creek can be inferred by comparing sediment lethal concentrations (96-h LC_{50}) among different salmonid species and by examining the cumulative effect of high temperatures on this stress. Comparisons indicated that lake whitefish are most sensitive to suspended sediment, while chinook salmon are stressed more than rainbow trout but less than coho salmon (Table 2). Concentrations even along the river margins (>150 $mg \cdot L^{-1}$) probably disrupted feeding, growth, and social behaviour, caused some fish displacement, and increased susceptibility to disease. Compounding influences from high or low temperatures also greatly increased salmonid sensitivity to sediment (Stober et al. 1981; Newcombe and MacDonald 1991; Servizi and Martens 1991). During August, sediment sensitivity in the Fraser River probably increased 30-fold as water temperatures increased to 16–19°C (Stober et al. 1981; Servizi and Martens 1991) despite a 60–80% (margins to thalweg) decline of sediment concentration.

Newcombe and MacDonald (1991) proposed a "severity of impact index" to assess impacts of suspended sediments on aquatic organisms. When their model was criticized as being too general and without boundaries (Gregory et al. 1993), their revisions produced another model specific to juvenile salmonids (MacDonald and Newcombe 1993). Their salmonid index is calculated from the product of exposure concentration and duration (index = $0.845 \cdot \log_e(mg \cdot L^{-1} \cdot h^{-1}) - 0.591$) and it predicted severe sublethal effects and some mortalities for indices of 9 and 10, respectively. During most years, salmonids in the Fraser River are exposed to an index value ≥10 using mean concentrations at Marguerite (500 $mg \cdot L^{-1}$ for 528 h; Carson 1988) or an index of ≥9 using concentrations from the river margin (150 $mg \cdot L^{-1}$ for 528 h). This suggested that salmonids in the Fraser River are under extreme stress and that if exposure duration is as important as sediment concentration, then clear tributaries and side-channels may be critical for chinook survival. Juvenile chinook salmon, rainbow trout, and mountain whitefish would probably avoid the sediment concentrations in the Fraser River, enter the clear waters of Hawks Creek, and tolerate the high densities there.

Densities of chinook salmon in Hawks Creek were greater than reported values for other juveniles of >50 mm FL, possibly causing downstream displacement and the short residency for juveniles. In Hawks Creek, the average density exceeded $0.7 \cdot m^{-2}$ seined for the summer of 1990 (Table 1) and maximum densities were $>0.76 \cdot m^{-2}$ wetted area during August 1990 and $>1.1 \cdot m^{-2}$ during August 1984 (396/0.8)/443 m^2; Levings et al. 1985). Maximum densities in nonnatal tributaries ranged from 0.12 to $0.56 \cdot m^{-2}$ in the Nechako watershed (5 m mean width; Russell et al. 1983) and from 0.06 to $0.68 \cdot m^{-2}$ in the lower Fraser Valley (Murray and Rosenau 1989). Densities declined from 0.4 to $0.04 \cdot m^{-2}$ along the margin of the Nechako River during the summers of 1985, 1986, and 1991 (2.0 and $0.2 \cdot m^{-1}$ per 5 m of river margin; Nechako River Project 1987; Brown et al. 1994). Average densities of $0.18 \cdot m^{-2}$ were observed in the Fraser estuary (Levy and Northcote 1982). Reported summer densities for Idaho rivers were $0.56–0.70 \cdot m^{-2}$ (Hillman et al. 1987) and $0.1–0.5 \cdot m^{-2}$ (Everest and Chapman 1972). Juvenile chinook salmon can be displaced downstream when the densities observed at Hawks Creek occur (Chapman and Bjornn 1969; Lister and Genoe 1970; Hillman et al. 1987), thus providing a possible reason for their short residence time there.

Juvenile chinook salmon probably did not establish feeding territories in Hawks Creek. They remained only ~9 d which might not be enough time to establish and defend a territory (Chapman and Bjornn 1969; Healey 1991). Densities were also near levels where juvenile salmonids tended to form aggregations (reviewed by Heggenes et al. 1993). Previous studies indicated that defence of feeding territories usually caused displacement and emigration of the smaller individuals (Chapman and Bjornn 1969; Hartman et al. 1982; Healey 1991), but large fish have a shorter residence time than small fish in Hawks Creek.

During the summer, the size of juvenile chinook salmon increased at a smaller or similar rate to that of other streams. In Hawks Creek, mean FLs of 60, 70, and 78 mm were achieved by early July, late August, and September 30, respectively (Table 1). Juveniles rearing in the Nechako and Stuart rivers had attained 70 mm before June 30 and 76 mm by July 30 (Nechako River Project 1987; Brown et al. 1994). They had increased to >80 mm by late July in nonnatal tributaries of the lower Fraser Valley (Murray and Rosenau 1989) and in the Big Qualicum River (Lister and Genoe 1970). The pattern of FL increases in Hawks Creek was similar to those of other Fraser River tributaries such as the Chilcotin River (Delaney et al. 1982), Nechako tributaries (Russell et al. 1983), and Slim Creek (J.S. Macdonald, Department of Fisheries and Oceans, West Vancouver, B.C., personal communication). The pattern of increase would also be similar to that of Willow and Horsefly rivers (Fraser tributaries) when a 2-wk later emergence of fry is considered for these colder rivers (Murray et al. 1981; Whelen et al. 1981). Since the growth of juvenile chinook using Hawks Creek appeared slower or similar to that of other streams, we concluded that food was not the major attraction for salmonids entering it.

Changes of habitat preference by fish and changes in the habitat (declining water level and temperature) probably caused the size-selective emigration among juvenile chinook salmon and the autumn exodus of all salmonids from Hawks Creek. Four studies have indicated that age 0^+ chinook salmon select deeper and faster water as they grow (Chapman and Bjornn 1969; Everest and Chapman 1972; Hillman et al. 1987; Nechako River Project 1987). Fish of >60 mm FL preferred depths of ≥0.6 m and velocities of $\geq 20\ \mathrm{cm \cdot s^{-1}}$ (Hillman et al. 1987; Nechako River Project 1987). Except during the June 29–30 storm, water depth and velocity were <0.7 m and $< 20\ \mathrm{cm \cdot s^{-1}}$ in Hawks Creek pools, and they were declining during the summer. Juvenile chinook salmon and steelhead trout (Chapman and Bjornn 1969; Hillman et al. 1987) and mountain whitefish (Hagen 1970) began moving from small tributaries to rivers or lakes in September as stream temperatures declined. Most fish had left summer habitat when temperatures were <5°C and entered deeper water or water associated with cover (woody debris, boulders). Substantial evidence has been presented that temperature changes triggered the changes in behaviour (Chapman and Bjornn 1969). Suitable winter habitat is very limited in Hawks Creek.

Juvenile salmonids become difficult to catch during severe winter conditions because they shelter within any coarse substrate during daylight (reviewed by Heggenes et al. 1993). During the winter, daylight pole-seining and electrofishing captured only a fraction of the fish that were caught at night in the Nechako River (C. Shirvell, Department of Fisheries and Oceans, Nanaimo, B.C., personal communication). This phenomenon probably was not the reason for the reduced catch in Hawks Creek during November because catch began declining much earlier, stream temperature still exceeded 2°C, and substrates in the lower third of the study reach were too small to shelter ~75-mm juveniles.

Juvenile chinook salmon may have been less abundant in Hawks Creek during 1990 than in other years because numbers were reduced by the June 29–30 storm and sediment concentrations in the Fraser River were much lower in 1990 than in earlier years (Carson 1988). Sediment levels exceeded $1000\ \mathrm{mg \cdot L^{-1}}$ for 12 of 16 years at the Marguerite site (Carson 1988), while it was only $656\ \mathrm{mg \cdot L^{-1}}$ during 1990. Daily mean concentrations also exceeded $500\ \mathrm{mg \cdot L^{-1}}$ for ≥22 d during 10 of the 16 previous years. Thus, there was less stress inducing chinook salmon to enter Hawks Creek during 1990 than in previous years. During August 1984, chinook salmon were 1.5 times more abundant in Hawks Creek than during August 1990 (Levings et al. 1985).

The use of small nonnatal tributaries of the upper Fraser River by juvenile chinook salmon is probably a response to adverse environmental conditions within the mainstem Fraser River. Juvenile chinook salmon appeared to rear and grow for some time in nonnatal tributaries of the lower Fraser Valley (Murray and Rosenau 1989) and the Nechako River (Russell et al. 1983), but small clear streams like Hawks Creek appeared to be used as refuge habitat from high sediment concentrations found within the Fraser River during their downstream migration. Feeding is probably less inhibited in these clear streams, but the short-term and seasonal residency and the high fish densities in Hawks Creek support the refuge concept.

It is of concern that many of the sources of clear water flowing into the turbid Fraser River would not be protected as chinook habitat because they lack spawning adults and incubating eggs. Although these small streams lack chinook salmon for much of the year, their importance as refuge habitat and sources of food for migrating juveniles cannot be overlooked. Small clear streams such as Hawks Creek must be considered an important component in the life cycle of chinook salmon which originate from the upper Fraser River. Water from Hawks Creek and many similar streams is extracted to irrigate agricultural land or their watersheds are managed for timber production (G. Kosakoski, Department of Fisheries and Oceans, Kamloops, B.C., personal communication). These small chinook streams should be identified, characterized, properly evaluated, and ultimately protected.

Acknowledgements

We thank E. Choromanski and T.J. Brown for their assistance at Hawks Creek and L. Smith for analysis of the sediment samples. Comments by R.S. Gregory, C.D. Levings, J.S. Macdonald, J.A. Servizi, and two anonymous reviewers were used to improve the manuscript.

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Effects of Experimental and Cultural Lake Acidification on Littoral Benthic Macroinvertebrate Assemblages

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A simple method for the assessment of littoral benthic macroinvertebrate (BMI) assemblages in lakes was developed at the Experimental Lakes Area (ELA) in northwestern Ontario and applied to 64 lakes in central Ontario. The presence (1) or absence (0) of BMI taxa was established at five sites on each lake, using a kick-and-sweep net technique. Summing presence/absence scores across sites ranked the importance of each taxon in each lake on a scale of 0 to 5. Relationships between the BMI assemblages were assessed using nonmetric multidimensional scaling (NMDS), based upon the Kendall's τ correlation matrix. Correlations between NMDS dimension 1 and 2 scores and environmental variables identified factors that may structure BMI assemblages. The BMI assemblages of three experimentally acidified and seven reference lakes at the ELA were correlated strongly with lake pH. The BMI assemblage structure of central Ontario lakes was predicted by lake area and sensitivity to acidification (NMDS dimension 1) and by lake elevation (NMDS dimension 2). The BMI assemblages of small or Ca-poor and acidic lakes include fewer oligochaetes, mayflies, and *Cryptochironomus* and *Stictochironomus* (chironomids) and more Odonata, Trichoptera, *Chironomus*, *Conchapelopia*, *Microtendipes*, and *Procladius* (chironomids), and *Crangonyx* (Amphipoda) than other central Ontario lakes.

On a mis au point, dans la région des lacs expérimentaux du nord-ouest de l'Ontario, une méthode simple d'évaluation des groupes de macro-invertébrés benthiques d'eau douce (MIB), que nous avons appliquée à 64 lacs de la partie centrale de l'Ontario. On a déterminé la présence (1) ou l'absence (0) des taxons qui composent ces groupes à cinq emplacements dans chaque lac en soulevant la vase avec les pieds et en passant un filet. On a déterminé l'importance de chaque taxon, dans chaque lac, en additionnant le total des présences à toutes les stations, et en attribuant une cote de 0 à 5. On a évalué les rapports entre les groupes de MIB en procédant à une analyse multidimensionnelle non métrique qui s'appuie sur la matrice de corrélation τ de Kendall. Les corrélations entre les scores obtenus pour les dimensions 1 et 2 de l'analyse multidimensionnelle et les variables environnementales ont permis de trouver des facteurs qui peuvent permettre de détecter une structure dans les groupes de MIB. Ceux des trois lacs expérimentalement acidifiés et ceux des sept lacs de référence de la région des lacs expérimentaux vivaient en forte corrélation avec le pH du lac. La structure des groupes de MIB des lacs du centre de l'Ontario a été prévue à partir de la superficie du lac et de la sensibilité à l'acidification (dimension 1 de l'analyse multidimensionnelle), ainsi qu'à partir de l'altitude du lac (dimension 2). Les groupes de MIB trouvés dans les lacs de petite dimension ou pauvres en Ca ou acides contiennent moins d'oligochètes, d'éphéméroptères et de *Cryptochironomus* et de *Stictochironomus* (chironomidés) et davantage d'odonates, de trichoptères, de *Chironomus*, de *Conchapelopia*, de *Microtendipes* ainsi que de *Procladius* (chironomidés), and *Crangonyx* (amphipodes) que les autres lacs de la partie centrale de l'Ontario.

Received January 28, 1993
Accepted December 9, 1993
(JB771)

Reçu le 28 janvier 1993
Accepté le 9 décembre 1993

Many lakes in central Ontario, Canada, experience acid deposition expressed as total S loadings, in excess of 1.0 g $S \cdot m^{-2} \cdot yr^{-1}$ (Neary and Dillon 1988). This level of loading is causing the acidification of many lakes and streams. Neary and Dillon (1988) showed that the mean pH and alkalinity of lakes in various regions of Ontario were a function of the total S deposition rate. Dillon et al. (1987) reported that about 20% of some 1800 lakes surveyed in central Ontario between 1981 and 1985 had alkalinity <25 $\mu eq \cdot L^{-1}$ and are considered sensitive to acid deposition. Many lakes in regions receiving acidic precipita-

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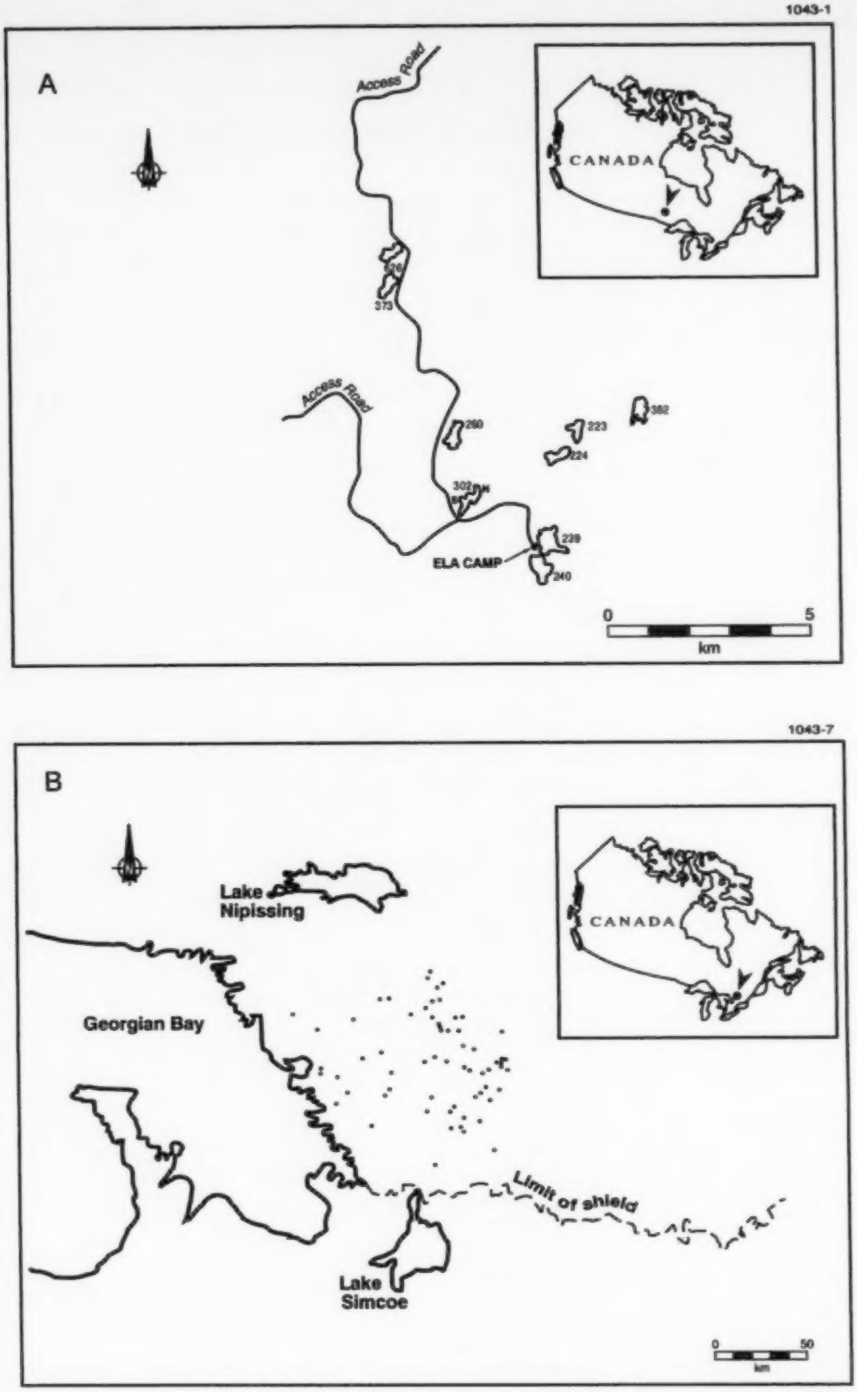
1043-1
A
Access Road
CANADA
376
373
Access Road
260
223
382
224
302
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S
239
ELA CAMP
240
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5
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1043-7
B
Lake Nipissing
Georgian Bay
CANADA
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Lake Simcoe
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FIG. 1. Locations of the study lakes at (A) the ELA and (B) in central Ontario. The inset map of Canada shows the general locations of the ELA and central Ontario sites.

tion experience strong seasonal acidification events in the littoral zone (Gunn and Keller 1984; Baird et al. 1987; Galloway et al. 1987; Hasselrot et al. 1987; Gubala et al. 1991).

The effects of lake acidification on aquatic biota have been widely discussed (Schindler 1988; Muniz 1991). Many benthic macroinvertebrate (BMI) taxa including insects, crustaceans, and molluscs are intolerant of low pH (Økland and Økland 1986). Most studies of BMIs, however, describe

TABLE 1. Selected physical and chemical characteristics of ELA lakes. Chemical data are ice-free season means for epilimnetic water, 1987. The pH of L302n was reduced to 5.5 by HCl additions beginning in July 1987.

	L302n	L302s	L223	L224	L239	L240	L626	L260	L373	L382
Ca ($mg \cdot L^{-1}$)	2.11	2.63	2.87	1.85	3.24	2.67	2.43	2.65	3.14	2.19
Mg ($mg \cdot L^{-1}$)	0.68	0.74	0.67	0.52	0.99	0.92	0.68	0.73	0.74	0.70
Na ($mg \cdot L^{-1}$)	0.84	1.03	1.17	0.89	1.46	1.33	1.07	1.14	1.13	1.12
K ($mg \cdot L^{-1}$)	0.38	0.38	0.33	0.37	0.77	0.72	0.53	0.56	0.48	0.47
Cl ($mg \cdot L^{-1}$)	2.59	0.68	0.32	0.22	0.48	0.59	0.70	0.36	0.31	0.35
SO_4 ($mg \cdot L^{-1}$)	4.76	10.7	10.5	3.43	5.32	4.75	2.50	2.42	3.06	3.30
DOC ($mg \cdot L^{-1}$)	5.5	3.8	3.0	2.8	5.8	6.0	6.1	5.2	3.8	7.1
pH	5.8	4.8	5.4	7.0	7.2	7.1	7.2	7.1	7.3	7.0
Lake surface area (ha)	12.8	10.9	30.2	25.4	56.1	44.1	22.0	32.4	28.3	37.3
Maximum depth (m)	13	10	15	27	35	14	15	15	22	12

acidification effects on individual taxa (Nero and Schindler 1983; Servos et al. 1985; Stephenson and Mackie 1986) rather than assemblages or communities. This contrasts with studies on phytoplankton (Kwiatkowski and Roff 1976; Yan and Miller 1984; Findlay and Kasian 1986; Kelso et al. 1986; Earle et al. 1987; Siegfrid et al. 1989a), zooplankton (Sprules 1975; Roff and Kwiatkowski 1977; Carter et al. 1986; Kelso et al. 1986; Siegfrid et al. 1989b), and fish (Rahel and Magnuson 1983; Somers and Harvey 1984; Bendell and McNicol 1987a) which evaluate entire assemblages, representing many individual lakes. When BMIs have been studied as assemblages, they have been either identified only to coarse taxonomic levels (Collins et al. 1980) which may obscure effects or studied under extreme acid loadings, and concurrently with high trace metal loadings (Bendell and McNicol 1987b).

Several important BMIs found in central Ontario lakes are known to be sensitive to acidification. These include crayfish (*Orconectes* spp.) (Malley 1980; Berrill et al. 1985), the amphipod *Hyalella azteca* (Stephenson and Mackie 1986), the gastropod *Amnicola limosa* (Mackie and Flippance 1983; Servos et al. 1985; Shaw and Mackie 1990), and several species of mayfly (Allard and Moreau 1987; Hall and Ide 1987). Mechanisms of toxicity have been proposed for several invertebrate taxa (Havas 1980; Wood and Rogano 1986; France and Stokes 1987). The loss of taxa from BMI assemblages should create vacant niches, available for colonization by new or previously suppressed taxa, yet little is known about how BMI assemblages respond to acidification or the roles of physiological tolerance and competitive interactions in the development of characteristic assemblages at low pH. Various contaminants have been shown to modify BMI assemblages in predictable and well-characterized ways (Wiederholm 1984). Therefore, changes in lake chemistry that exceed the tolerance of some invertebrate species, or that lead to substantial modifications of either their food and habitat resource or the abundance of fish and invertebrate predators, will lead to modifications in BMI assemblage structure that can be characterized.

This paper documents the development of methods for assessing and comparing BMI assemblages, using lakes that have been experimentally acidified at the Experimental Lakes Area (ELA) in northwestern Ontario, Canada. We subsequently evaluate the littoral BMI assemblage structure of central Ontario lakes and discuss how the BMI taxa comprising the assemblage respond to physical and chemical environmental gradients.

Methods

Development of Methods

Site description

A pilot study was conducted using three experimentally acidified (Lakes 223, 302 north, and 302 south, hereafter abbreviated L223, L302n, and L302s) and seven reference (Lakes 224, 239, 240, 260, 373, 382, and 626, abbreviated L224, etc.) lake basins at the ELA (Fig. 1A). Table 1 presents selected physical and chemical characteristics of these lakes. Because strong acid loadings are low in the ELA (Neary and Dillon 1988), these lakes showed little evidence of anthropogenic acidification prior to experimental manipulation. As the chemical histories of the acidified lakes are well documented (Schindler et al. 1980; Turner et al. 1987), and all lakes had similar chemistry prior to experimental acidification, they are particularly suitable for the development and testing of benthic survey methods. We assumed that as a consequence of their geographic proximity and their chemical and physical similarity, these lakes supported similar littoral BMI assemblages prior to experimental acidification.

Methods development

The sampling and enumeration of BMIs is a difficult, expensive, and time-consuming process. Even under ideal conditions, quantitative data are often imprecise and poorly reproducible. For this study of the littoral zone, where substrate heterogeneity is great, quantitative sampling was not considered feasible. As an alternative, qualitative methods were adapted from those of plant ecologists (Pielou 1977; Kenkel 1986) facing similar problems in the description of plant assemblages.

The goal of sampling was to describe the littoral BMI assemblage of each lake. To do this, we sampled a specified number of locations within the lake, scored the presence (1) or absence (0) of each taxon at each site, and summed the taxon scores for all sites to derive a rank index of taxonomic importance (TI) for each taxon in each lake. With a description of the littoral BMI assemblage of each lake, it is possible to compare lakes. We used a rank correlation coefficient (Kendall's τ, Kendall 1955) as an index of similarity between lakes (Ghent 1987) and ordinated lakes on the basis of a similarity matrix comparing all lake pairs, using nonmetric multidimensional scaling (NMDS) (Shepard 1962a, 1962b; Kruskal 1964a, 1964b). The starting configuration of the NMDS analysis was selected by metric multidimensional scaling (Wilkinson 1990). NMDS is a procedure for fitting a set of points in a space such that the rank distances between points correspond to a given set of similarities or dissimilarities between a set of objects (Wilkinson 1990). Kenkel and Orloci (1986) compared the utility of a number of ordination techniques by evaluating their ability to correctly describe the structure of known data sets. They concluded that NMDS is superior to other methods, particularly when high degrees of species turnover are present in the test data. All statistical procedures were performed using SYSTAT (Wilkinson 1990).

Lake sampling began with the selection of sampling stations from a map of the lake. In each lake basin, a compass rose was established near the centre, with transects intersecting the shore at the eight major compass points. Sampling stations were identified by randomly selecting a number between 1 and 360. This "spin" number was used to rotate the eight compass points clockwise from their proper locations (i.e., with a spin number of 27, true north would be rotated 27° clockwise). Five sampling stations were then selected at random from these eight points, the remaining three locations providing redundancy should any of the five selected stations prove impossible to sample (i.e., a vertical drop off to depth >1 m). If a lake contained more than one main basin, additional compass roses could be used to ensure adequate coverage of the entire littoral zone. Islands were disregarded.

Benthic macroinvertebrates were collected from the littoral stations using a kick-and-sweep net technique. A 12-in. triangular, 200-μm-mesh sweep net was worked back and forth along a transect from shore to 1-m depth, while the substrate was being vigorously disturbed by kicking. In addition, other identifiable habitats (weed beds, organic debris, fallen trees, silt, sand, gravel, boulder, bedrock) within 10 m on either side of the transect point were spot-sampled. Finally, individual rocks and logs were overturned, and any adhering or clinging invertebrates were removed with forceps. The total search time at each station was approximately 15 min. All of the collected material was deposited in a 200-μm mesh sieve box (Mackie and Qadri 1971), sieved, and returned to the laboratory for sorting. The debris was hand-sorted, live, for benthic macroinvertebrates. No attempt was made to quantitatively remove all the invertebrates from the sample. The prime objective while sorting was to collect specimens of as many different taxa as possible. We regard this sampling method to be robust because the quantitative efficiency of the method for each taxon was not important. Capturing a single specimen of a taxon at a given site was sufficient to record its presence. Invertebrates removed from samples were stored in 70% ethanol and identified to the lowest taxon possible (Usinger 1956; Klemm 1972; Wiggins 1977; Pennak 1978; Hiltunen and Klemm 1980; Mackie et al. 1980; Kowalyk 1981; Burch 1982; Stimpson et al. 1982; Wiederholm 1983; Merritt and Cummins 1984).

Methods testing

To evaluate the precision and reproducibility of our methods, we initially sampled seven lakes (L302s, L223, L302n, L224, L382, L373, L239) at the ELA between 3 June and 1 July 1987. L239 and L302s were sampled five times each, with an independent randomization of sampling station locations each time. L223, L302n, L224, L373, and L382 were each sampled twice, again with an independent randomization of sampling stations each time. After sorting and identification of the BMIs, the data were ordinated in two ways. First, an ordination was performed on all 20 data sets showing how each collection compared with other collections from that lake and how the lakes compared with each other. Second, all the collections from each lake were pooled, TI scores were standardized to a maximum value of 5, and an ordination of seven lakes was performed on the basis of all of the available samples. A cluster analysis (complete linkage algorithm), also based on the Kendall's τ correlation matrix, was used to link points hierarchically in the ordinations. This linkage is represented graphically by a set of contours, with each successive contour admitting one point to each cluster.

During the summer of 1987, after the initial BMI assemblage samples were collected, the pH of L302n was reduced from 5.8 to 5.5 by adding hydrochloric acid (D. Cruikshank, Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Man., personal communication). To assess the impact of this acidification on the BMI assemblage, another survey of eight lakes (L626, L260, L382, L240, L223, L239, L302n, L302s) was conducted between 16 and 18 October 1987. Five stations were sampled on each lake, the invertebrates were sorted and identified, and the lakes were ordinated as previously described.

The demonstration that acidic lakes separate from a population of reference lakes in ordination space shows that BMI assemblages have been distinctly modified by acidification. However, the biologically important information that shows which taxa are impaired or stimulated by acidification is suppressed. To recover this information, we used a nonparametric correlation coefficient (Spearman) to measure the correlation between TI scores of each taxon in each lake and the lake's location in NMDS dimensions 1 and 2. Generally, we considered correlation coefficients with absolute value >0.40 to indicate a meaningful relationship between TI scores and NMDS dimension 1 or 2 score.

Application to Central Ontario Lakes

Site description

We selected 64 central Ontario lakes (Fig. 1B) from existing Ontario Ministry of the Environment (OME) records. Lakes were chosen on the basis of their water chemistry to give approximately equal representation to lakes in six alkalinity classes; −10 to 0, 0 to 10, 10 to 20, 20 to 40, 40 to 80, and >80 $\mu eq \cdot L^{-1}$. Lake areas were constrained between 1 and 200 ha to exclude both very small and very large lakes. Lakes near paved roads were avoided to minimize the effect of chemicals (primarily NaCl) used in deicing.

Central Ontario lake survey

Lakes were sampled between 3 October and 6 November 1987. As at the ELA, five sampling stations were randomly selected at each lake. At each station, a transect was sampled from 0- to 1-m depth, using a kick-and-sweep technique and a 200-μm-mesh sweep net. Additional habitats within 10 m of the transect point were spot-sampled. Water samples for chemical analysis were usually collected at both midlake and shoreline stations. Midlake samples were generally a 5-m-tube composite sample whereas littoral zone samples were a 1-m-tube composite. Most littoral zone samples were analyzed for pH, alkalinity, and conductivity. Midlake samples and generally one littoral sample were analyzed for pH, alkalinity, conductivity, dissolved organic carbon (DOC), SO_4^{2-}, Cl^-, Ca^{2+}, Mg^{2+}, Na^+, K^+, total P,

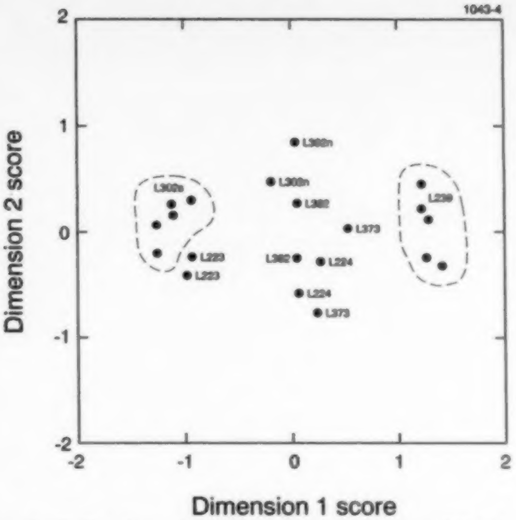

FIG. 2. Ordination of BMI assemblages from acidified and nonacidified ELA lakes, based upon five stations per sample.

total Kjeldahl nitrogen (TKN), and total Al. All analyses were performed in OME laboratories.

Benthic invertebrate samples were hand-sorted within 24 h of collection and stored in 70% ethanol until they were identified. Identification was to the lowest taxonomic level possible by experienced taxonomists using published keys, normally to the generic or specific level. A reference collection of selected specimens was examined independently to validate the identifications.

To explore relationships between BMI assemblages and environmental conditions, we first simplified the taxonomic data by eliminating rare taxa (those having TI scores, summed across all lakes, not exceeding 10). This procedure reduced the taxonomic matrix from 169 to 65 taxa. The ordination of lakes on the basis of 65 taxa differed little from an ordination including all taxa. To perform the ordination, we calculated a similarity matrix, based upon the taxonomic data for all lake-pair combinations, using Kendall's τ coefficient. This matrix was used as the basis for a two-dimensional NMDS ordination of the lakes. Individual lake scores in NMDS dimensions 1 and 2 were compared with the physical and chemical characteristics of the lakes by stepwise multiple linear regression (MLR). To simplify the number of variables included in the model, and to satisfy the statistical requirement that predictor variables in stepwise MLR be independent and uncorrelated, the full set of variables (ln-transformed, with the exception of pH, to improve the normality of the data) was first reduced by principal components analysis (PCA). Varimax rotations were used to enhance the separation of chemical variables onto factors, without sacrificing their orthogonality. The NMDS dimension 1 and 2 scores, which are also orthogonal and approximately normally distributed, were then regressed against the factor (F) scores for each lake. This approach satisfies the statistical requirements of MLR, but sacrifices the unambiguous identification of individual physical or chemical variables as correlates of BMI assemblage structure. Fortunately, factors can usually be assigned a general interpretation. After MLR using the F scores, we returned to the original environmental data and selected variables strongly correlated with each of the F scores to construct a regression model using the fewest

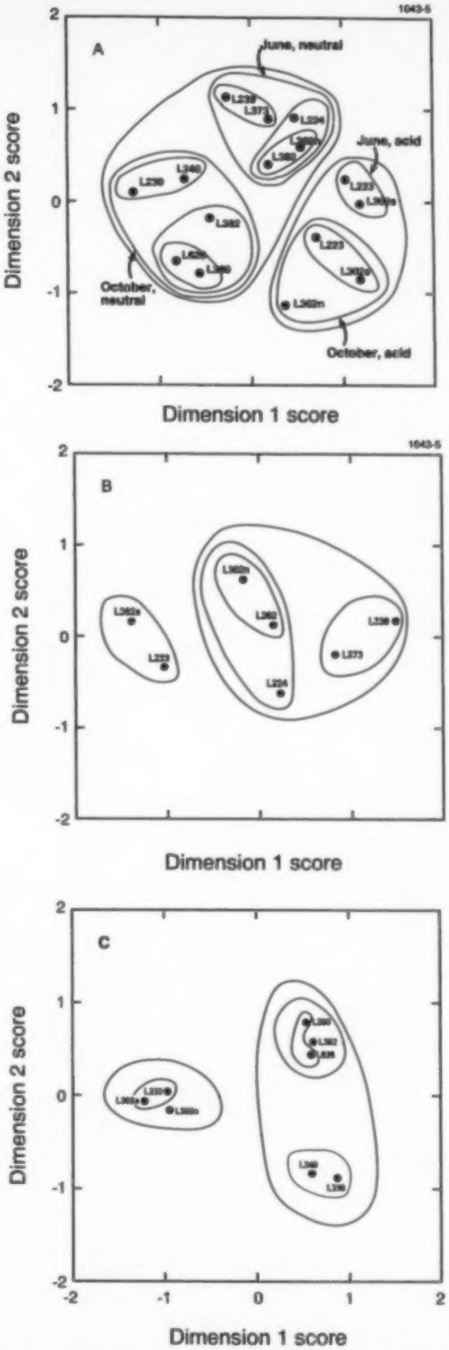

FIG. 3. Ordination of BMI assemblages from acidified and nonacidified ELA lakes in (A) June and October 1987, (B) June 1987, and (C) October 1987. Contours indicate the linkages between lakes identified by cluster analysis. L302n clusters with the reference lakes in June (pH = 5.8), but joins the acidic lakes in October (pH = 5.4).

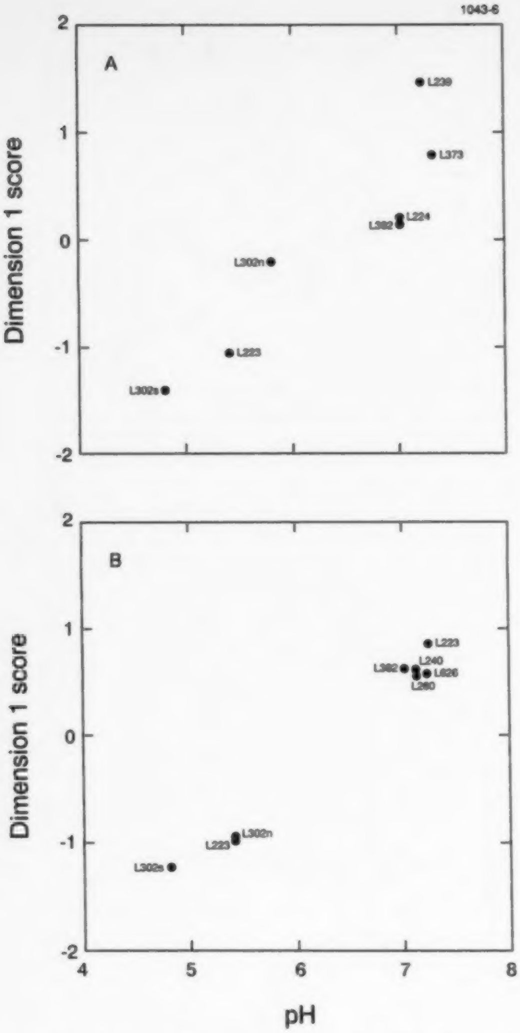

FIG. 4. Correlations between lake pH and NMDS dimension 1 score for lakes sampled in (A) June 1987 (Spearman's $r = 0.96$) and (B) October 1987 (Spearman's $r = 0.78$).

and least correlated variables to reproduce the model using F scores. The significance criterion for entry to, or removal from, the regression models was $p = 0.10$.

To evaluate the invertebrate taxa responsible for structuring the NMDS ordination of lakes, we used a Spearman correlation coefficient to identify those taxa having TI scores correlated with lake location in NMDS dimensions 1 and 2.

Results and Discussion

Methods Development

As an evaluation of the methods, a set of acidified and reference lakes was sampled at the ELA in June 1987. Each lake was sampled either twice (L302n, L223, L224, L382, L373) or five times (L302s, L239). For each lake, samples were processed independently by either the senior author (M. Stephenson) or an assistant (B. Koenig). Ordination of these data (Fig. 2) shows that lakes group consistently in the first dimension of ordination, with occasional separations in the second dimension. These separations were not consistently a function of the identity of the investigator, or of sampling date.

Impacts of experimental acidification at ELA

The experimentally acidified lakes at the ELA were sampled on two occasions in 1987. In June 1987, the acidified lakes (L223, L302s, L302n) had mean pH values of 5.4, 4.8, and 5.8, respectively. Reference lakes (L382, L224, L239, L373) had mean ice-free season pH values ranging from 6.6 to 7.1. In October 1987, the acidified lakes had mean pH values of 5.4, 4.8, and 5.5, respectively (L302n having been made acidic, pH < 5.6, by addition of HCl). We performed three ordinations on these data. The first ordination included all lakes, sampled in both seasons (Fig. 3A). Cluster contours (complete linkage algorithm) indicate that the lakes separate first into acidic and circumneutral groups and secondarily separate by season into summer-sampled and fall-sampled lakes. The effect of season was expected, and resulted from the absence of many taxa from summer samples because of reproductive activity. These taxa may have been present in the study lakes as egg or early instar life stages that were either too small to capture or identify, or occupy zones other than the littoral at that time. The absence of many taxa from samples collected in summer was a major factor in the decision to conduct the survey of central Ontario lakes in the fall. To isolate the effects of acidification, we performed ordinations on summer (Fig. 3B) and fall (Fig. 3C) data separately and base our subsequent analysis on these ordinations.

Because the lakes separated in ordination space largely along the first dimension (Fig. 3B and 3C), the correlation between the assumed driving variable (lake pH) and the response variable (dimension 1 score) was examined. Both in the summer, before L302n was acidified to pH 5.5, and in the fall, following acidification, lake position in the NMDS ordination (dimension 1), based upon the BMI assemblage structure, was a function of lake pH (Fig. 4).

Using Spearman rank correlation coefficients, we identified those taxa associated positively or negatively with NMDS dimension 1 score (Table 2). In general, BMI assemblage response to acidification at ELA can be characterized as involving the loss of TI by gastropods (*Gyraulus*, *Physella*, *Amnicola*), mayflies (*Stenonema*, *Stenacron*, *Ephemera*, *Leptophlebia*), some Trichoptera (*Mystacides*, *Helicopsyche*, *Lepidostoma*, *Ceraclea*, *Agarodes*), some Coleoptera (*Stenelmis*, *Dubiraphia*, *Uvarus*, *Hygrotus*) and Hydracarina and Amphipoda (particularly *Hyalella*). Simultaneously, a suite of taxa including Hirudinea (*Helobdella*, *Mooreobdella*), Odonata (*Boyeria*, *Enallagma*, *Ischnura*, *Libellula*, *Ladona*, *Aeshna*, *Chromagrion*), some Trichoptera (*Oecetis*, *Limnephilus*, *Banksiola*), and chironomids (*Tanytarsus*, *Glyptotendipes*, *Dicrotendipes*, *Psectrocladius*, *Microtendipes*, *Tribelos*, *Micropsectra*, *Paratendipes*, *Ablabesmyia*, *Chironomus*, *Paratanytarsus*) exhibit increased TI in acidic lakes. This change in taxonomic structure occurred rapidly, as evidenced by the shift in ordination space exhibited by L302n when it was acidified from pH 5.8 to 5.5 during the summer of 1987 (Fig. 3A)

TABLE 2. Taxonomic responses to experimental acidification at the ELA. Tabulated values are Spearman correlation coefficients between TI scores and NMDS dimension 1 scores for the summer and fall 1987 samples. Only correlations with absolute value >0.50 are presented. Negative correlations indicate those taxa that are more abundant in acidic lakes.

Taxon		Response	
Group	Genus	Summer	Fall
Platyhelminthes	*Dugesia*	0.509	
Oligochaeta	*Stylaria*	0.771	
Hirudinea	*Helobdella*	−0.593	−0.619
	Mooreobdella	−0.643	
	Nephelopsis	0.538	
Gastropoda	*Gyraulus*	0.612	0.651
	Physella	0.612	0.592
	Amnicola		0.600
Plecoptera	*Haploperla*		0.577
Ephemeroptera	*Stenonema*	0.889	0.964
	Stenacron	0.618	0.927
	Ephemera	0.802	0.592
	Leptophlebia		0.626
Odonata	*Boyeria*	−0.730	
	Enallagma	−0.670	
	Ischnura	−0.612	−0.660
	Libellula	−0.657	−0.784
	Ladona	−0.535	
	Aeshna		−0.830
	Chromagrion		−0.845
Corixidae		−0.612	
Trichoptera	*Mystacides*	0.927	0.889
	Helicopsyche	0.802	0.756
	Oecetis	−0.741	
	Lepidostoma	0.808	
	Ceraclea	0.612	
	Limnephilus		−0.693
	Banksiola		−0.655
	Agarodes		0.825
Coleoptera	*Stenelmis*	0.519	
	Dubiraphia		0.756
	Gyrinus		0.592
	Dineutus	−0.896	
	Uvarus	0.612	0.592
	Hygrotus	0.612	
Diptera	*Palpomyia*		−0.551
	Culicoides		0.536
	Alluaudomyia		−0.639
	Chrysops		−0.620
	Hexatoma		0.845
Chironomidae	*Polypedilum*	0.643	
	Procladius	0.800	
	Tanytarsus	−0.739	−0.679
	Glyptotendipes	−0.716	
	Dicrotendipes	−0.829	−0.651
	Psectrocladius	−0.741	
	Microtendipes	−0.679	−0.618
	Tribelos	−0.808	−0.727
	Micropsectra	−0.612	
	Paratendipes	−0.757	
	Ablabesmyia		−0.544
	Chironomus		−0.822
	Paratanytarsus		−0.784
	Pagastiella		0.646
	Eukiefferiella		0.770
Hydracarina	sp. A		0.677
	sp. B	0.599	
	sp. E	0.889	0.674
	sp. F	0.883	0.776
	sp. H	0.791	
	sp. J	0.749	
Amphipoda	*Hyalella*	0.867	0.866
	Crangonyx		0.613

TABLE 2. (*Concluded*)

Central Ontario Survey

Water chemistry

A comparison of alkalinity measurements from littoral and midlake sites (Fig. 5) showed no systematic differences in water chemistry. Similar results were obtained for total inorganic P, conductivity, and pH. Therefore, the chemistry of water samples collected at the midlake sites was used exclusively in the following analyses to represent all sites in the lake. Although the lakes were selected from historical data to represent six alkalinity classes, they did not conform to the expected distribution when sampled in 1987 (Fig. 6). Fewer lakes than expected were observed in the lowest alkalinity classes. Consequently, the data set included very few lakes classified as acidic (alkalinity < 0, pH < 5.6). Our failure to sample acidic lakes, however, does not compromise the study design or objectives. We sampled gradients of lake morphometry and chemistry in central Ontario. Our sample included lakes with pH ranging from 7.11 to 4.92 (Table 3). The study lakes provide ample scope to test hypotheses concerning BMI assemblage response to environmental gradients. Summary statistics for lake morphometry and midlake water chemistry are given in Table 3. Generally the lakes have low concentrations of dissolved salts, are nutrient poor, and have little DOC. Most are mesotrophic to dystrophic, although some clearwater lakes with low ($<10\ \mu g \cdot L^{-1}$) P concentrations ([P]) are oligotrophic, and others with high ($>30\ \mu g \cdot L^{-1}$) [P] are eutrophic according to Wetzel (1975).

PCA (with varimax rotations) of the data from the 62 lakes for which complete water chemistry and physical data matrices were available reduced the 15 measured variables to seven factors incorporating 84.8% of the total variance in the data set. These seven factors (Table 4) are interpreted to represent lake sensitivity to acidification, dystrophy (DOC, TKN), [SO_4^{2-}], [Cl^-], area, elevation, and total [P], respectively. The results of this analysis closely resemble results from an earlier assessment of water chemistry and lake morphometry in central Ontario (Stephenson and Mackie 1988). In both analyses, lake sensitivity to acidification emerged as the first factor (F1), and lake area was independent of lake acidification status. In the present study, the degree of dystrophy measured [DOC] and [TKN] and was independent of trophic state (F7) as measured by total [P].

Correlation of lake ordination with water chemistry

Ordination of the taxonomic data by NMDS produced a plot (Fig. 7) showing good separation of lakes in both dimensions, and without any clumping of points. The Kruskal stress value of the final solution is 0.259, which is reasonable considering the dimensionality of the data.

TABLE 3. Summary statistics for water chemistry and lake morphometry for the central Ontario lakes surveyed in this study.

Variable	Mean[a]	Minimum	Maximum
Alkalinity (μeq$\cdot$L^{-1})	69	−12.4	316
Mg (mg$\cdot$L^{-1})	0.61	0.24	2.02
pH	6.25	4.92	7.11
Conductivity at 25°C (μS)	27.9	18.0	232.0
Ca (mg$\cdot$L^{-1})	2.20	1.20	4.60
K (mg$\cdot$L^{-1})	0.41	0.16	1.04
Na (mg$\cdot$L^{-1})	0.77	0.42	6.12
DOC (mg$\cdot$L^{-1})	3.96	1.80	9.10
TKN (μg$\cdot$L^{-1})	284.0	130.0	540.0
Total Al (μg$\cdot$L^{-1})	11.9	1.0	124.0
SO_4 (mg$\cdot$L^{-1})	6.28	1.14	10.70
Cl (mg$\cdot$L^{-1})	0.46	0.05	26.0
Lake surface area (ha)	28.8	2.2	198.9
Lake surface elevation above sea level (m)	339.7	205.6	465.0
Total P (μg$\cdot$L^{-1})	11.9	3.95	35.5

[a] All means are geometric, except for pH, which is arithmetic.

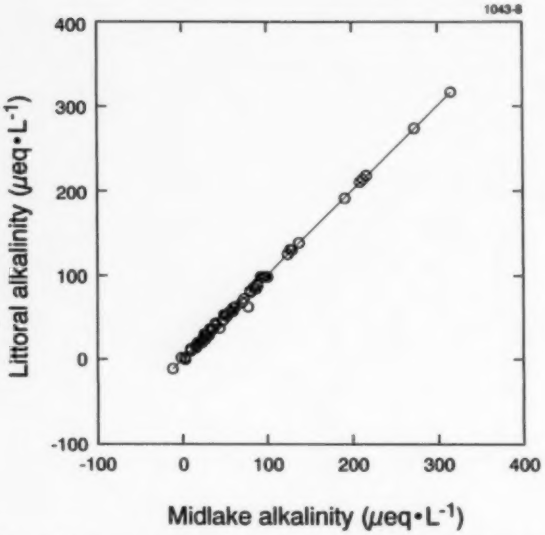

FIG. 5. Measured alkalinity in central Ontario lakes based upon samples collected at littoral or midlake sites. The slope and intercept of the least-squares fitted line are not significantly different from 1 and 0, respectively.

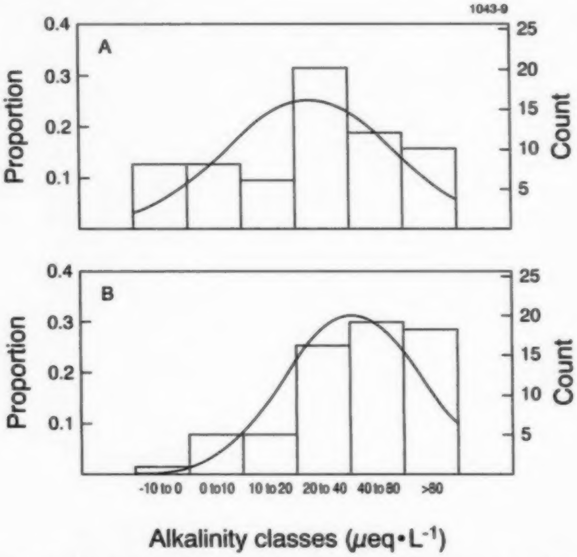

FIG. 6. Alkalinity classes (A) expected and (B) observed during the central Ontario survey in 1987.

Using stepwise MLR, we predicted lake locations in NMDS dimension 1 using the PCA reductions (F scores) of the lake chemistry and morphometry measurements. Sixty-two lakes were available for this analysis. Three factors (F1) representing lake sensitivity to acidification; F5, lake area; and F2, degree of dystrophy) were retained in the stepwise model (Table 5), accounting for 53.6% of the variation in assemblage structure as measured in NMDS dimension 1. Attempts to predict NMDS dimension 2 scores were less successful; however, stepwise MLR identified F6 (lake elevation) as a significant ($p = 0.002$) predictor of dimension 2 score, accounting for 13.4% of variation in lake location in that dimension (Table 6).

To confirm our interpretation of the significance of principal components, we performed a stepwise MLR analysis on NMDS dimension 1 scores using the original data (log-transformed) for lake chemistry and morphometry as predictor variables. The best model was consistent with the PCA results and included Ca, area, and DOC (Table 7). These variables predicted 52.0% of the variance in NMDS dimension 1 scores. Likewise, regression analysis of lake elevation versus location in NMDS dimension 2 confirmed the interpretation of F6, the regression statistics being virtually identical.

The predictive power of lake sensitivity to acidification, lake area, and degree of dystrophy (as measured by factor scores) for BMI assemblage structure (as measured by NMDS dimension 1 score) is illustrated in Fig. 8. Although there was no relationship between lake area and pH (Spearman's r = 0.056), lakes that score positively on NMDS dimension 1 tend to be both small and acid sensitive whereas lakes having

TABLE 4. Eigenvector coefficients from a PCA (varimax rotations) of water chemistry and basin morphometry for 62 central Ontario lakes. Underlining indicates variables strongly correlated ($r > 0.5$) with individual factors.

Variable[a]	F1	F2	F3	F4	F5	F6	F7
Alkalinity	0.928	−0.140	−0.088	0.029	0.030	0.033	−0.067
Mg	0.902	0.012	0.202	0.078	−0.066	−0.136	0.030
Conductivity	0.889	0.000	0.181	0.267	0.033	−0.062	0.103
pH	0.862	0.091	−0.114	0.045	0.079	0.027	−0.149
Ca	0.835	0.002	0.227	−0.038	0.106	−0.076	0.018
Na	0.736	−0.152	0.060	0.429	0.072	0.038	0.084
K	0.688	−0.130	0.081	0.157	0.103	0.013	0.030
TKN	0.053	−0.935	−0.076	−0.016	−0.179	0.061	0.178
DOC	0.135	−0.871	−0.064	−0.020	−0.040	0.102	0.221
Al	−0.282	−0.530	0.020	0.037	0.033	0.084	0.174
SO_4	0.157	0.099	0.963	−0.031	−0.042	−0.177	−0.043
Cl	0.205	0.034	−0.038	0.969	−0.036	0.099	0.045
Area	0.092	0.158	−0.040	−0.030	0.971	0.133	−0.032
Elevation	0.073	0.125	0.181	−0.103	−0.140	−0.954	−0.062
Total P	−0.006	−0.438	−0.053	0.067	−0.042	0.076	0.881
%variance explained	34.0	14.8	7.5	8.3	6.9	6.9	6.3

[a] Units for all variables are as in Table 3.

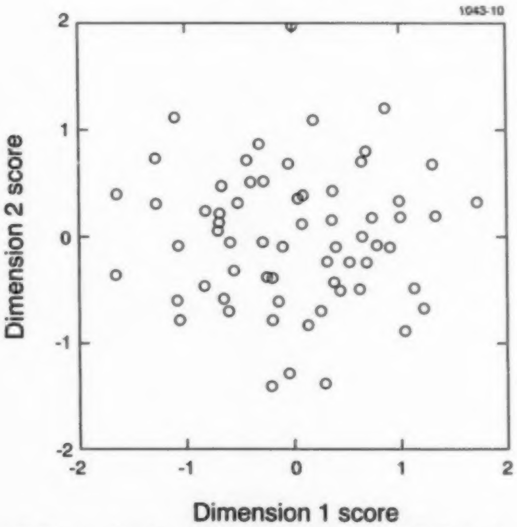

FIG. 7. Scatterplot showing lake locations in NMDS dimensions 1 and 2.

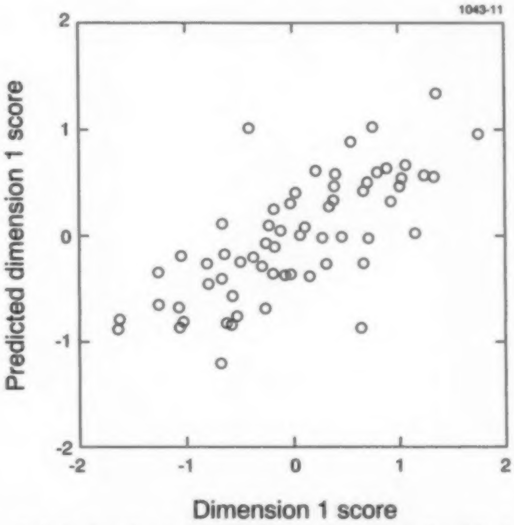

FIG. 8. Lake location in NMDS dimension 1 as predicted by lake sensitivity to acidification, lake area, and degree of dystrophy.

negative NMDS dimension 1 scores are larger and circumneutral. The degree of dystrophy explained only a small residual fraction of the total variance once sensitivity to acidification and lake area had been taken into account.

Taxonomic determinants of lake location in ordination

On the basis of Spearman correlation coefficients (Table 8), a total of 10 taxa had higher TI in lakes ordinating positively in NMDS dimension 1 whereas a further seven taxa exhibited the opposite trend (i.e., Spearman's $r \geq 0.4$). A similar analysis, comparing the TI of individual taxa in lakes having positive NMDS dimension 2 scores with those having negative dimension 2 scores, identified two taxa having higher TI in lakes with positive dimension 2 scores whereas five taxa had higher TI in lakes with negative dimension 2 scores.

Taxa identified as having higher or lower TI across NMDS dimension 1 or 2 are summarized in Table 8 and Fig. 9. In addition to the Spearman correlation coefficient approach (Table 8), we used simple inspection of the data to identify nonmonotonic relationships between TI and NMDS dimension 1 and 2 scores (Fig. 9). Generally, taxonomic associations with dimension 1 are similar to associations seen in the pilot study of experimentally acidified lakes at the ELA. Notably, several taxa of Ephemeroptera, the elmid beetle *Dubiraphia*, the oligochaete *Lumbriculus*, and the amphipod *Hyalella* have lower TI in the smaller, or acid-sensitive lakes ordinating positively in dimension 1. Likewise, several taxa of Odonata, Chironomidae, the dipteran *Chrysops*, the trichopteran *Banksiola*, and others have higher TI in these lakes than in lakes ordinating negatively in dimension 1.

TABLE 5. Stepwise MLR of NMDS dimension 1 scores using factor scores from water chemistry and lake morphometry as predictor variables.

Variable	Coefficient	SE	t	p	% variance explained
Intercept	−0.008	0.070	−0.112	0.911	
F1	−0.409	0.070	−5.825	<0.001	27.2
F5	−0.368	0.070	−5.239	<0.001	21.9
F2	−0.165	0.070	−2.353	0.022	4.5

Analysis of variance

Source	Sum of squares	df	Mean square	F	Probability
Regression	20.106	3	6.702	22.3	<0.001
Residual	17.429	58	0.300		

$n = 62$, $r = 0.732$, $r^2 = 0.536$

TABLE 6. Stepwise MLR of NMDS dimension 2 scores using factor scores from water chemistry and lake morphometry as predictor variables.

Variable	Coefficient	SE	t	p
Intercept	0.000	0.078	−0.004	0.997
F6	−0.240	0.079	−3.043	0.003

Analysis of variance

Source	Sum of squares	df	Mean square	F	Probability
Regression	3.513	1	3.513	9.26	0.003
Residual	22.756	60	0.379		

$n = 62$, $r = 0.366$, $r^2 = 0.134$

TABLE 7. Stepwise MLR of NMDS dimension 1 scores using lake area, Ca, and DOC as predictor variables.

Variable	Coefficient	SE	t	p
Intercept	1.684	0.416	4.051	<0.001
Ca	−1.329	0.250	−5.321	<0.001
Lake area	−0.345	0.079	−4.383	<0.001
DOC	0.377	0.192	1.967	0.054

Analysis of variance

Source	Sum of squares	df	Mean square	F	Probability
Regression	19.525	3	6.508	21.0	<0.001
Residual	18.010	58	0.311		

$n = 62$, $r = 0.721$, $r^2 = 0.520$

Figures 9B–9T show the TI of selected individual taxa across the gradient of NMDS dimensions 1 and 2.

It is less easy to generalize about taxa responsible for lake ordination in dimension 2, as no clear taxonomic or physicochemical associations emerge. The TI scores of five taxa (*Cladotanytarsus*, *Amnicola*, *Zalutschia*, *Arrenurus*, and *Dugesia*; Fig. 9U–9X) were strongly correlated with NMDS dimension 2 score. Lake elevation is a weak predictor of lake position in NMDS dimension 2. Possibly some taxa have had limited historical access to the higher elevation lakes. Martin and Chapman (1965) concluded that the distributions of several crustacean and fish species in Algonquin Park were influenced by the ancient limits of inundation by Glacial Lake Algonquin, at a maximum elevation of 385 m. In the Dorset area, on the basis of the distribution of the shrimp *Mysis relicta*, the limit of inundation was between 329 m (Harp Lake, *M. relicta* present) and 336 m (Blue Chalk Lake, *M. relicta* absent). Regional differences in the present elevations of Glacial Lake Algonquin strandlines may be caused by differential isostatic rebound. Using an elevation of 335 m as a dividing criterion, about half (35) of the 64 lakes surveyed are located above the strandline. Lakes located at higher elevation should lack taxa that have low potential for dispersal; however, many of the taxa responsible

TABLE 8. Summary of taxonomic associations with NMDS dimensions 1 and 2 identified in central Ontario lakes. Tabulated values are Spearman correlation coefficients between TI scores and NMDS dimensions 1 or 2. Only correlations with absolute value >0.40 are presented. Positive correlations indicate those taxa that are more abundant in acid-sensitive lakes.

Taxon		Response	
Group	Genus	Dimension 1	Dimension 2
Platyhelminthes	*Dugesia*		−0.402
Oligochaeta	*Lumbriculus*	−0.573	
Gastropoda	*Amnicola*		−0.607
Ephemeroptera	*Stenonema*	−0.509	
	Stenacron	−0.595	
	Eurylophella	−0.481	
Odonata	*Cordulia*	0.551	
	Ladona	0.643	
	Leucorrhinia	0.509	
	Macromia	−0.440	
	Gomphus		−0.411
Trichoptera	*Banksiola*	0.472	
	Pycnopsyche		0.409
Diptera	*Chrysops*	0.422	
Chironomidae	*Conchapelopia*	0.442	
	Procladius	0.603	
	Chironomus	0.560	
	Cryptochironomus	−0.412	
	Microtendipes	0.489	
	Stictochironomus	−0.642	
	Zalutschia		0.536
	Cladotanytarsus		−0.607
Hydracarina	*Arrenurus*		−0.575
Amphipoda	*Crangonyx*	0.464	

for lake location in NMDS dimension 2 (Table 8) have winged adult stages, so dispersal or colonization pathways should not restrict taxonomic access to high-elevation lakes. Moreover, examination of the TI scores of selected taxa as a function of lake elevation does not suggest any relationships. From the large unexplained variation in dimension 2 scores, it is possible that there may be unmeasured environmental variables such as substrate or vegetation types that correlate with dimension 2.

Our inability to separate the effects of lake size and sensitivity to acidification suggests that either there is some direct interaction between these two factors or their independent effects are similar. Similar independent effects may exist if changes in lake area affect certain groups of BMIs more than others. Large lakes may have littoral zones exposed to water movement resulting from wind action and waves. In these lakes, the littoral zone may be more streamlike than in smaller lakes, favouring mayflies, elmid beetles, and other taxa often associated with streams. Conversely, interactive effects between lake area and sensitivity to acidification are also possible. Although a rank correlation of lake area versus pH indicates no association in the study lakes, small lakes often have proportionally more shoreline in comparison with their water mass. Consequently, the effects of seasonal or transient acid pulses caused by precipitation events and meltwater in spring may be more severe in small lakes than in large lakes. We do not have evidence to support or refute either of these hypotheses.

The best predictive model for NMDS dimension 1 score, using environmental variables, includes $[\mathrm{Ca}^{2+}]$, lake area, and [DOC]. Similar models using pH and total inflection point alkalinity in place of $[\mathrm{Ca}^{2+}]$ were less successful. Although the model including $[\mathrm{Ca}^{2+}]$ was the best predictor of BMI assemblage structure, we cannot conclude that $[\mathrm{Ca}^{2+}]$ structures BMI assemblages. $[\mathrm{Ca}^{2+}]$ and pH are correlated, a source of difficulty in multiple regression models. Furthermore, both pH and alkalinity are temporally more variable than $[\mathrm{Ca}^{2+}]$. Consequently, with "grab" water samples, $[\mathrm{Ca}^{2+}]$ may be a better predictor of NMDS dimension 1 scores than pH or alkalinity because $[\mathrm{Ca}^{2+}]$ more closely reflects time-integrated conditions.

Physiological interactions between acidity and Ca metabolism are well documented. At least some species present in Precambrian Shield lakes, including the snails *A. limosa* and *Campeloma decisum*, are adapted to the soft-water environment (McKillop and Harrison 1972); however, biota living in acid-stressed environments are generally less able to obtain and retain ions, including Ca^{2+} (Malley 1980; Wood and Rogano 1986). Many trace metals, which are mobilized from sediments and watersheds undergoing acidification, are more toxic when the ambient $[\mathrm{Ca}^{2+}]$ is low. Several taxa (*Hyalella*, *Amnicola*) identified as being rare in lakes sensitive to acidification are known to be affected directly by acidification (Servos et al. 1985; France and Stokes 1987; Shaw and Mackie 1990), rather than being limited by low $[\mathrm{Ca}^{2+}]$. The crayfish *Orconectes virilis* was eliminated from previously suitable habitat in L223 during experimental acidification (France 1987). Thus, the acidification of Ca-poor envi-

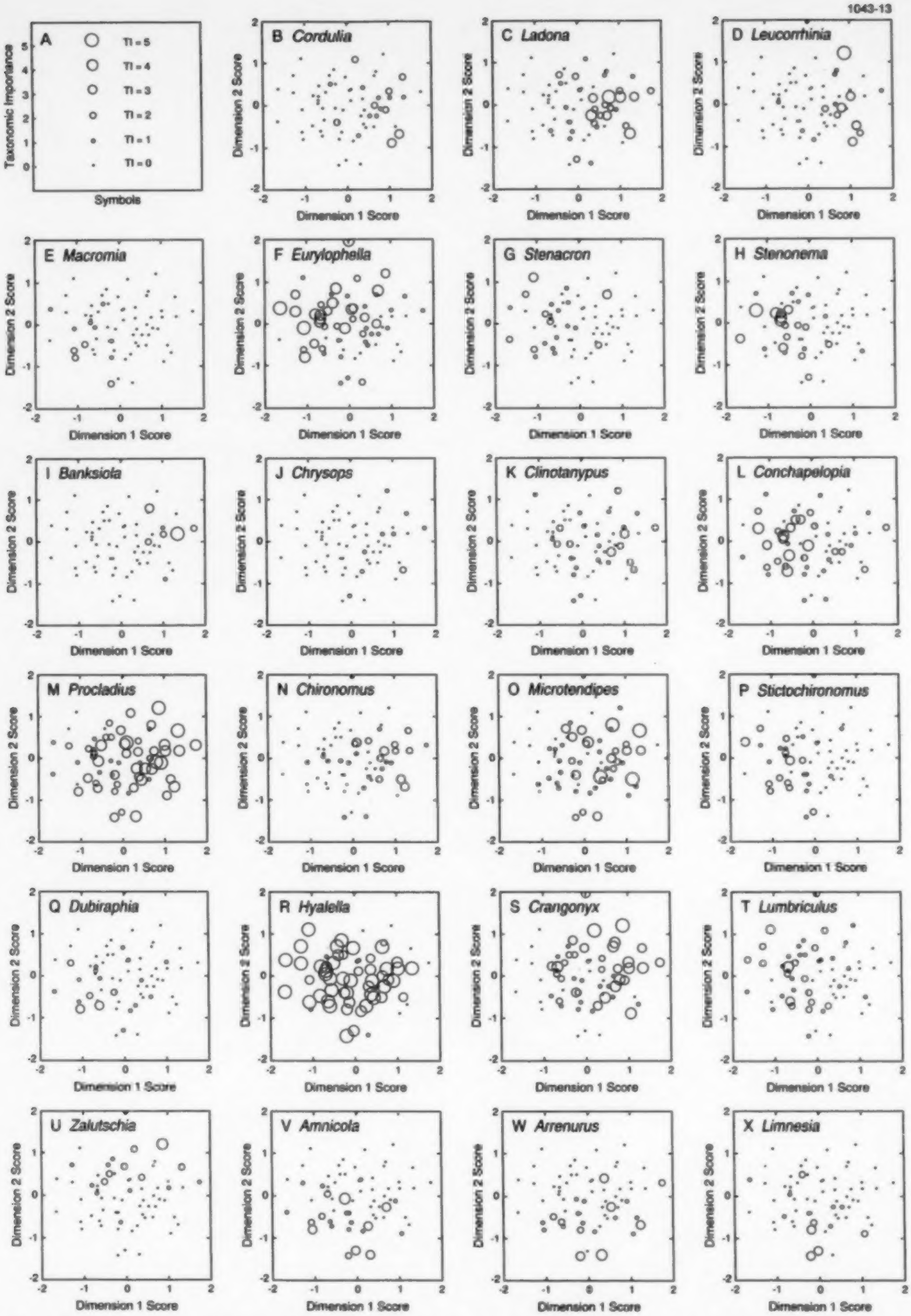

FIG. 9. (A) Key indicating symbol size associated with TI score in subsequent panels; (B–X) TI scores (indicated by symbol size) of individual taxa across NMDS dimensions 2 and 1.

ronments results in selective species loss, likely due to pH effects (H^+ toxicity), trace metal toxicity, physiological ion balance problems, or the combined effects of these factors.

Relationship to other studies

Several previous studies have evaluated the impact of acidification on BMI assemblages of groups of lakes, and generalizations have emerged. Some groups of BMI taxa are conspicuously absent from acidic lakes. These include amphipods (*Gammarus*) (Økland and Økland 1980) in Europe, *Hyalella* (Stephenson and Mackie 1986) in North America, many species of Ephemeroptera (Sutcliffe and Carrick 1973; Engblom and Lingdell 1984; Raddum and Fjellheim 1984; Harvey and McArdle 1986; Weatherley and Omerod 1987), Gastropoda and other molluscs (Sutcliffe and Carrick 1973; Roff and Kwiatkowski 1977; Collins et al. 1980; Eriksson et al. 1980; Raddum and Fjellheim 1984; Harvey and McArdle 1986; Bradt and Berg 1987; Morris 1988), and some Coleoptera (Elmidae) (Sutcliffe and Carrick 1973; Weatherley and Omerod 1987).

Acidic lakes are frequently characterized by abundant planktonic or nektonic insects including *Chaoborus*, Notonectidae, Corixidae, and Gyrinidae (Eriksson et al. 1980; Henrikson and Oscarson 1981; Dermott 1985; Bendell 1986; Bendell and McNicol 1987b; Morris 1988). Other large invertebrate taxa, particularly Odonata and Megaloptera, also tend to show increased abundance and biomass in acidic lakes (Eriksson et al. 1980; Hildrew et al. 1984; Dermott 1985; Bradt and Berg 1987; McNicol et al. 1987). Many of these changes are considered responses to the absence of fish from severely acidified lakes (Bendell and McNicol 1987b; McNicol et al. 1987). Benthic macroinvertebrate assemblages subject to predation by fish have lower abundance and biomass, and dominant taxa tend to be smaller than in assemblages not preyed upon by fish (Gilliam et al. 1989). Although we have no measure of the fish assemblages present in the central Ontario study lakes, and some species have doubtless been lost from some lakes, we do not believe that fish have been totally eliminated from any of them as a result of acidification.

The changes observed in the BMI assemblages of central Ontario lakes are more subtle than those seen in acidic lakes, yet they are consistent with both the generalized responses discussed above and with changes seen in the experimentally acidified lakes in the ELA. Table 8 and Fig. 9 record decreased TI of *Hyalella*, *Stenacron*, *Stenonema*, *Eurylophella*, *Dubiraphia*, and some Hydracarina with increasing NMDS dimension 1 score whereas several Odonata, Chironomidae, and the trichopteran *Banksiola* increase in TI. *Leptophlebia*, unchanged in TI across NMDS dimension 1, has been observed to be relatively tolerant of acidification in Scandinavian lakes (Raddum and Fjellheim 1984) and Ontario streams (Hall and Ide 1987), although it was eliminated from severely acidified lakes at the ELA. The amphipod *Crangonyx laurentianus* is characteristic of small acid-sensitive to dystrophic lakes on the Canadian Shield (Bousfield 1958). The chironomid *Procladius* was among a suite of chironomids found to be more abundant in an acidifying Pennsylvania lake than in reference lakes (Bradt and Berg 1987) whereas the amphipod *Hyalella* and the snail *Amnicola* were reduced in abundance. Thus, changes in the BMI assemblage structure of weakly acidified central Ontario lakes, reflected in NMDS dimension 1 scores, appear to be evidence of an early response to acidification, the association with lake size suggesting that small lakes experience more damage from episodic acidification events than large lakes.

Conclusions

We have shown that a simple assessment technique, based upon the presence or absence of taxa at randomly selected stations, can characterize the littoral BMI assemblage of Canadian Shield lakes. Ordination, using NMDS, is an efficient and robust way to infer the effects of lake acidification. Using NMDS, we were able to correlate dimension 1 score with the chemical variable (pH) responsible for modifying BMI assemblage structure of ELA lakes. Our technique is inexpensive, robust, and suitable for addressing broad questions regarding the effects of environmental stressors on regional water resources.

An assessment of the BMI assemblages of 64 central Ontario lakes subject to strong acid deposition shows that assemblage structure is correlated with environmental gradients. The strongest response primarily reflects lake sensitivity to acidification and lake area, but it was not possible to isolate taxonomic responses to these parameters independently, or to specific chemical parameters. Small or acid-sensitive lakes support BMI assemblages different from those in larger or well-buffered lakes. Broadly consistent with observations from the experimentally acidified lakes at the ELA, *Hyalella*, *Lumbriculus*, and several Ephemeroptera, Chironomidae, and Trichoptera are reduced in TI whereas *Crangonyx*, several genera of Odonata, and some Trichoptera and Chironomidae have increased TI in acid-sensitive lakes. These observations suggest that many central Ontario lakes exhibit early signs of biological damage resulting from acid deposition.

Acknowledgements

M. Stephenson received an NSERC (Canada) Visiting Laboratory Fellowship, co-funded by the Ontario Ministry of the Environment and the Department of Fisheries and Oceans. Thanks are extended to D. Schindler, I. Davies, R. Hall, and N. Yan for advice and encouragement, R. Young, M. Shaw, B. Bilyj, and W. Morton for taxonomic identification, B. Koenig, M. Baker, S. Brown, S. Bailey, J. Darling, C. Peach, P. Welch, and D. Ming for assistance with field collections, and especially to P. Dillon for his support and patience. The manuscript was much improved by the reviews of S. Kasian, R. Bailey, and an anonymous referee.

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A Possible Relict Population of *Mesodesma deauratum* (Turton):Bivalvia (Mesodesmatidae) from the Southeast Shoal, Grand Banks of Newfoundland

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Hutcheson, M.S., and P.L. Stewart. 1994. A possible relict population of *Mesodesma deauratum* (Turton):Bivalvia (Mesodesmatidae) from the Southeast Shoal, Grand Banks of Newfoundland. Can. J. Fish. Aquat. Sci. 51: 1162–1168.

Extremely dense, localized concentrations of Turton's wedge clam *Mesodesma deauratum* (Turton) were found in quantitative grab samples on poorly sorted, medium to fine, low organic content sands (total organic carbon < 0.05%) at depths of 44–51 m at a single location on eastern Southeast Shoal of the Grand Banks of Newfoundland. Mean densities ranged from 24 to 5890 individuals·m^{-2} and wet weight standing crop from 0 to 21.4 kg·m^{-2}. A peak standing crop of 69.4 kg·m^{-2} was observed in one grab. There was a strong bimodal size distribution (17–27 and 34–56 mm shell length) at the site, but the two size groups never occurred together. Based on external growth checks, the smaller individuals were 4–5 yr old and the larger ones 10 to more than 15 yr. This population is suggested to be a relict of shallow littoral populations which probably existed in the area in the late Wisconsinan glacial period.

On a trouvé des mésodesmes de Turton (*Mesodesma deauratum* (Turton)) en concentration très élevée et de manière localisée lors du prélèvement d'échantillons au hasard sur des sables à faible teneur en matières organiques, mal triés et de granulométrie moyenne à fine (carbone organique total < 0,05 %) par 44 à 51 m de fond dans un seul secteur du Platier du Grand Banc de Terre-Neuve. La densité moyenne est comprise entre 24 et 5 890 individus·m^{-2}; la population exploitable, en poids frais, est comprise entre 0 et 21,4 kg·m^{-2}. Un échantillon a donné un maximum de 69,4 kg·m^{-2}. On observe une nette distribution bimodale des tailles (coquilles longues de 17 à 27 et de 34 à 56 mm), mais ces deux groupes ne sont jamais observés ensemble. Des signes extérieurs nous apprennent que les plus petits sujets ont entre 4 et 5 ans et que les plus gros ont entre 10 ans et plus de 15 ans. On pense que cette population pourrait être une relique de populations qui vivaient probablement en eaux côtières peu profondes à la fin de la période glaciaire wisconsinienne.

Received December 31, 1992
Accepted December 8, 1993
(JB744)

Reçu le 31 décembre 1992
Accepté le 8 décembre 1993

The two wedge clams, the Arctic (*Mesodesma arctatum* (Conrad)) and Turton's (*M. deauratum* (Turton)) found in the northwest North Atlantic, are typically shallow littoral dwellers (0 to 10–12 m) on exposed sandy areas tending to occur near inlets and bays (Merrill et al. 1978; Brêthes et al. 1986). It is of some interest then that high densities and biomass of *M. arctatum* were sampled by Russian fishery investigations from the Southeast Shoal of the Grand Banks of Newfoundland, a shallow, sandy bank about 380 km southeast of Newfoundland (Nesis 1965). We sampled the same area on five occasions during a year-long and more wide-ranging baseline survey of benthic invertebrate communities of the Grand Banks in connection with development of the Hibernia oilfield (Hutcheson et al. 1981). The purpose of that study was to describe the spatial and temporal characteristics of macroinvertebrate communities, dominant species, abundance and standing crop, trophic interactions, and relationships to environmental factors. The high biomass in one area of the mideastern Southeast Shoal reported by Nesis (1965), of which *M. arctatum* made up a large component, led us to place one of our stations there, which we subsequently sampled as part of the larger program. The sampling led to the discovery of high densities of *M. deauratum* but not the other species. This paper evaluates the significance of this finding and highlights the earlier Russian findings as well as other records which were not included in Merrill et al.'s (1978) review of the distributions of the two species. In addition, we report some characteristics of this population, including size, growth, spatial dispersion, and biomass. The findings represent an easterly extension of the range and a possible depth record for reproduction of the species. Speculation is also offered on the possibility that the population is a relict of geologically recent glacial advances.

Methods

As part of a baseline survey on the Grand Banks (Hutcheson et al. 1981), a series of seasonal samples (May, July, September, and November 1980 and February 1981) were

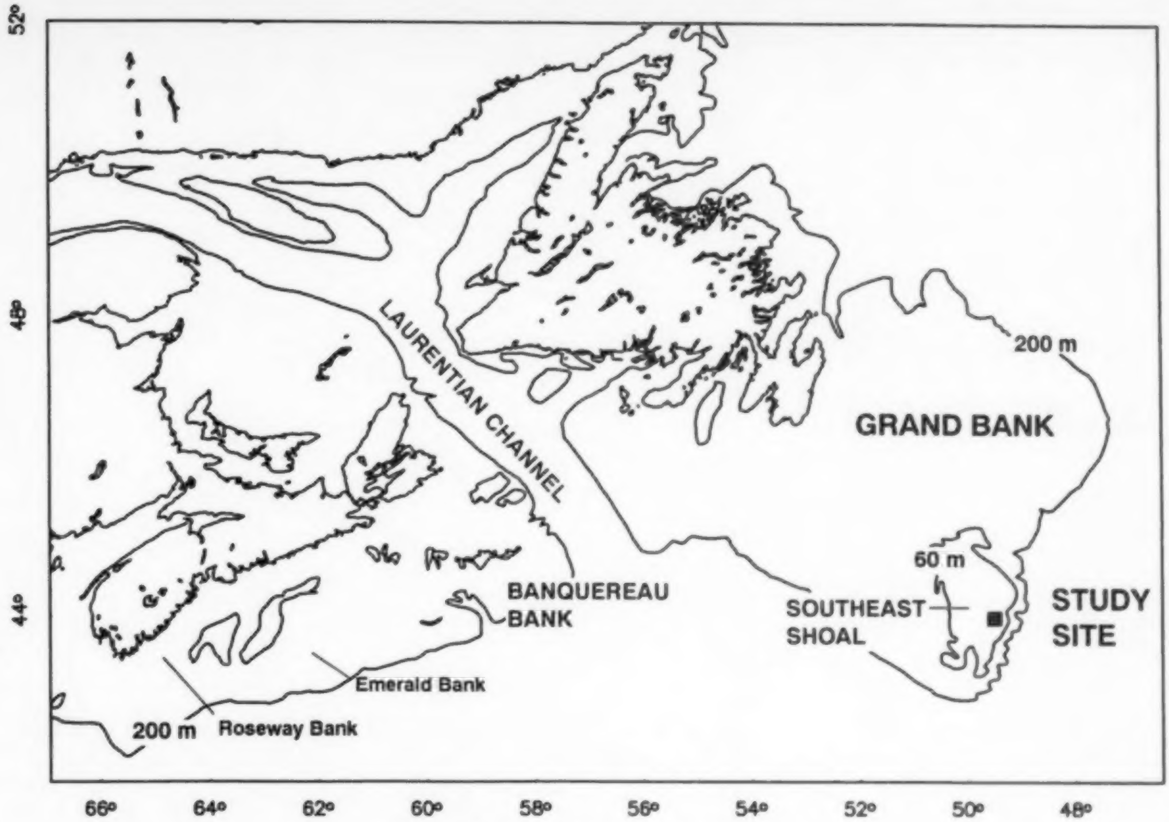

FIG. 1. Study site and locations cited in the text.

taken at a single station (Station 48, Hutcheson et al. 1981) on the Southeast Shoal of the Grand Bank (44°N, 49°30′W) (sampling depths 44–51 m) (Fig. 1). The station position was located and maintained using Loran coordinates, but owing to ship drift and the irregular nature of correction to Loran positions, the spacing between successive contacts with the bottom could not be estimated. Four or five 0.1-m^2 Van Veen grab samples and a 500-g sediment sample were taken on each sampling occasion. Samples were sieved through a 0.42-mm screen and fauna preserved in 10% Formalin in seawater buffered with hexamethylenetetramine or sodium borate. Sediment grain size was determined by dry sieving and pipette analysis, and total organic carbon (TOC) was measured with a LECO carbon analyzer. *Mesodesma deauratum* was also recovered from epibenthic sled samples (Hessler and Sanders 1967) taken as part of the routine benthic sampling at the station, but those data are not quantitative and thus are not included here. Water temperature, salinity, and chlorophyll *a* concentrations were also measured and reported in Hutcheson et al. (1981).

Either all the individuals or a subsample of 50 (whichever was smaller) from all the *M. deauratum* obtained on each visit were weighed. The following linear dimensions were also recorded: shell length in the anteroposterior axis, shell height (distance from the umbo to ventral shell margin, in the same plane as and perpendicular to length), and width (maximum distance through the left and right valves in the plane perpendicular to the length plane). Formalin-preserved wet weight was converted to fresh weight using a weight correction for shrinkage of 15% (Mills and Fournier 1979). Growth curves were generated by plotting shell height against age determined from counts of successive major growth rings, assuming that growth checks represent annual increments. Shell width to length ratios and shell length to height ratios were calculated. Frequency distributions of these ratios were tested for normality using the chi-square test for goodness of fit at $\alpha = 0.05$ (Sokal and Rohlf 1981). Nonnormal distributions were $\log_{10}$ transformed. Differences between means of smaller (see Fig. 2: defined as <30 mm shell length) and larger (defined as ≥30 mm shell length) clams were tested with the *t*-test.

Identification of *M. deauratum* was verified by Dr. D. Davis (Nova Scotia Museum, Halifax, N.S.) and Dr. A.S. Merrill (Harvard Museum of Comparative Zoology, Cambridge, Mass.), and specimens have been deposited in the collections of both museums and in the Canadian National Museum of Natural Sciences in Ottawa, Ontario.

Results

Physical Setting and Substrate

Water temperatures 10 m off the bottom at Station 48 ranged from 0.7 to 6.5°C, and salinity varied slightly between 32.4 and 33.1‰. The Southeast Shoal has the warmest bottom water temperatures of the entire Grand Banks from spring to fall (Loder 1991) and Station 48 is situated in an

TABLE 1. Physical characteristics of surficial sediments.

	% composition[a]												
	Gravel		Sand										
Date	Pebble and coarser	Granule	Very coarse sand	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay	Median grain size (mm)	Inman sorting index	TOC (%)	Depth (m)
May	3.6	4.9	8.3	28.7	49.9	4.6	0	0	0	0.46	0.9	<0.01	48
July	0	0	0.1	1.1	47.9	50.2	0.6	0	0	0.12	0.7	0.05	44
September	3.7	1.7	5.2	23.9	35.0	30.4	0.1	0	0	0.35	1.1	0.01	51
November	0	0	0.3	5.3	59.9	34.4	0.1	0	0	0.31	0.7	0.02	51

[a]Grade scales and size terminology used follow Wentworth (1922).

TABLE 2. Abundance and biomass of *M. deauratum* on the Southeast Shoal of the Grand Banks of Newfoundland.

	Densities (no.·m^{-2})								Biomass (g wet wt·m^{-2})						
	Replicate No.								Replicate No.						
Sampling date (1980–81)	1	2	3	4	5	$\bar{x}$	s	$s^2/\bar{x}$	1	2	3	4	5	$\bar{x}$	s
May	390	1550	10	0	—	488	731	1095	16.1	69.4	<0.1	0.0	—	21.4	32.9
July	6000	5190	6530	5840	—	5890	522	52	4.1	3.7	5.2	5.9	—	4.7	1.0
September	30	12 010	0	0	—	3010	6000	11 960	0.04	15.5	0	0	0	3.1	6.9
November	0	110	10	0	0	24	48	96	0	0.2	0	0	0	0	0.1
February	5980	820	20	8970	1410	3440	3864	4340	6.8	0.8	0	10.9	2.2	4.2	4.6

intermediate position between the area of warmest temperatures and the Labrador Current which flows south along the eastern edge of the Shoal. Substrate was predominantly fine to medium sand (Wentworth scale, median grain size 0.12–0.46 mm) occasionally containing coarse sand and a small amount of gravel-sized shell debris (Table 1). TOC content was <0.05%. Substrate characteristics were thus similar to fine to medium sand mixtures observed across the Southeast Shoal at that latitude (Hutcheson et al. 1981).

Distribution

The distribution of *M. deauratum* on the Grand Banks appears to be localized on the Southeast Shoal and possibly only on the eastern parts of it. The species was not observed in our other regular stations (13 stations in four areas) or in 45 single grab stations blanketing the Grand Banks at roughly half-degree longitude and degree latitude intervals throughout the whole of the Grand Banks (including seven at half-degree intervals on a transect across the Southeast Shoal along 44°N). The occurrence confirmed the localized concentrations of *M. arctatum* reported by Nesis (1965), which were the basis for our station selection. The cruises he reported sampled between approximately 20 stations on several lines impinging on the Southeast Shoal, generally east of 50°W and at or north of 45°N (Nesis 1965).

Size and Abundance

The striking feature of the occurrence of *M. deauratum* was the extremely high densities. Occasionally the abundance was so great that the grab was completely filled by live *M. deauratum*. Frequently empty shells of both *M. deauratum* and *M. arctatum* co-occurred with living *M. deauratum*, and occasionally beds of nonliving shells were sampled. Clams were distributed in two size groups, 17–27 and 34–56 mm shell length, but usually only individuals of the same size group were sampled on a given cruise (Fig. 2); the large size group was sampled only in May (Table 2) and by epibenthic sled in November (the latter group has not been included in this analysis). The small size group was sampled in July, September, November, and February 1981.

Mean wet weight standing crop of *M. deauratum* ranged from 0 to 21.4 kg·m^{-2} with a maximum in a single grab of 69.4 kg·m^{-2} (large clams, May). Standing crops over 3 kg·m^{-2} were common for grabs containing the smaller clams and the maximum standing crop for a single grab for this group was 15.5 kg·m^{-2} (Table 2).

The large size group, sampled in May, had an average density of 488 individuals·m^{-2} and a maximum in a single grab of 1550 individuals·m^{-2}. The patchy distribution at the site was evident, as the catch in two of the grabs was much smaller and a fourth grab sampled a bed of *M. deauratum* shells but no living individuals (Table 2).

Individuals in the smaller size group had a maximum mean density of 5890·m^{-2} in July and a peak density of 12 010·m^{-2} in one grab in September (Table 2). Smaller *M. deauratum* occurred in small numbers in two of five grabs in November, and the February sample contained from 20 to 8970 individuals·m^{-2} (mean 3440·m^{-2}, Table 2).

Spatial Dispersion

The statistical distribution of catch (Table 2) strongly suggested that the species occurred in high-density patches. There were either rather large or numerous patches in the sampling areas, as suggested by the occurrence of the same-sized individuals in replicate grabs on any one sampling trip even though the vessel may have drifted a considerable distance between the first and last replicate. The patchy distribution of the bivalves was illustrated by the high sampling variances associated with most visits to the station

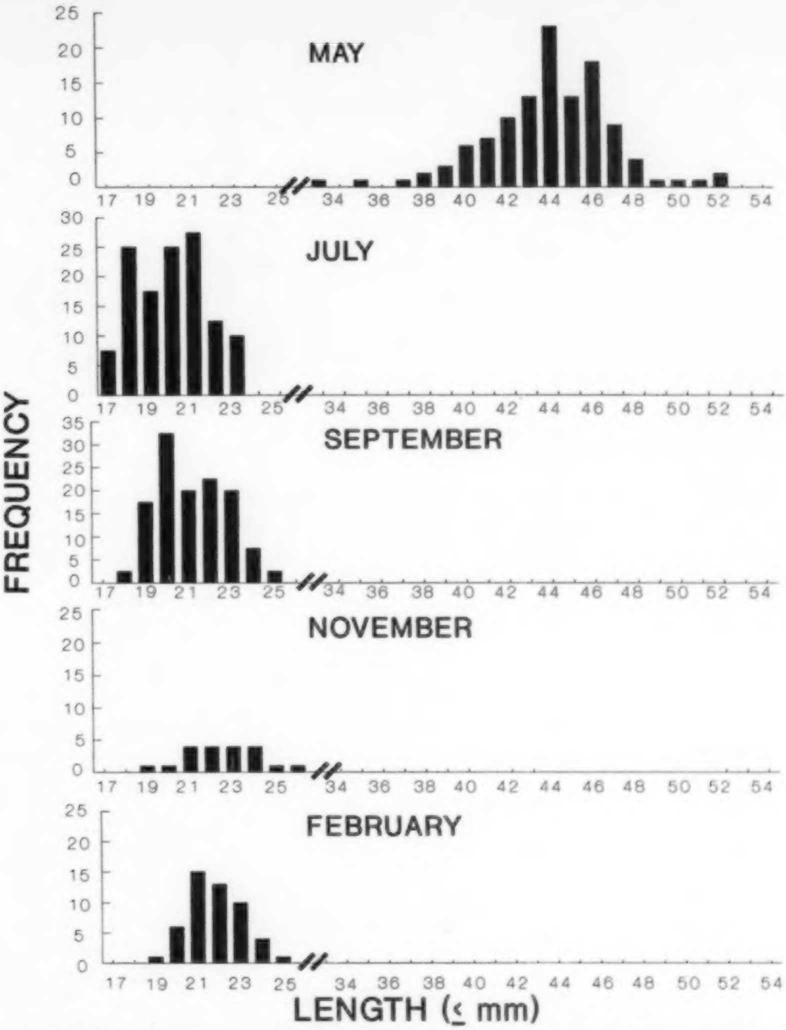

FIG. 2. Shell size frequency distributions of *M. deauratum* on the Southeast Shoal during 1980–81. Parallel hash marks denote a discontinuous x-axis scale.

and the fact that large and small size groups of clams did not occur together. Variance to mean ratios for abundance were high (ranging from 52 to 11 960, Table 2).

Growth Curves

Growth curves determined from growth checks were calculated separately for small and large clams (Fig. 3). The smaller size group of *M. deauratum* generally had four or five major growth rings and the larger ones 15 or 16 rings although some had as few as 10.

The two size groups had slightly different shell form, as indicated by a bimodal distribution of shell width to length ratios (Fig. 4). However, the shell height to length relationship was the same in the two groups, as evidenced by a unimodal lognormal distribution. The log-transformed ratios of shell width to length for smaller clams were significantly different ($t = 33.5$, $\alpha = 0.01$) than those for larger clams. These results indicate that the smaller individuals are not as wide in relation to their length as the larger clams.

Animal Communities

The larger *M. deauratum* at Station 48 were associated with a dense population of *Balanus crenatus* attached to *Mesodesma* shells, significant numbers of *Modiolus modiolus* (Table 3) in May (Hutcheson et al. 1981), and a single individual of *Mytilus edulis*. The community sampled with smaller *M. deauratum* was dominated by amphipods and polychaetes (Table 3). Various whelks including *Buccinum totteni*, *B. scalariforme*, *Colus pubescens*, and *C. stimpsoni* were observed in small numbers. *Buccinum totteni* occurred on all sampling occasions, while *B. scalariforme* and *C. pubescens* occurred only in May. *Colus stimpsoni* occurred only in the July sampling and was associated with the smaller *M. deauratum*.

Discussion

Turton's wedge clam *M. deauratum* has previously been reported to occur only in the St. Lawrence Estuary and

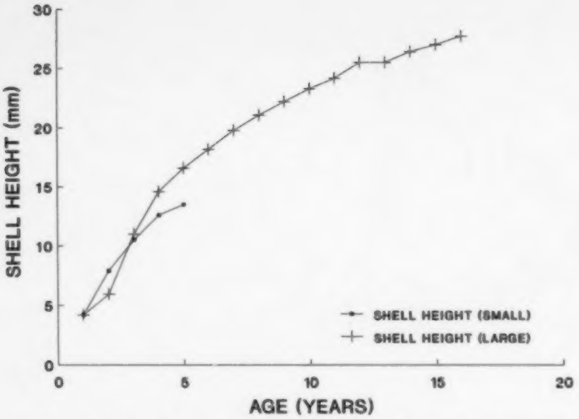

FIG. 3. Shell height versus age for small and large *M. deauratum.*

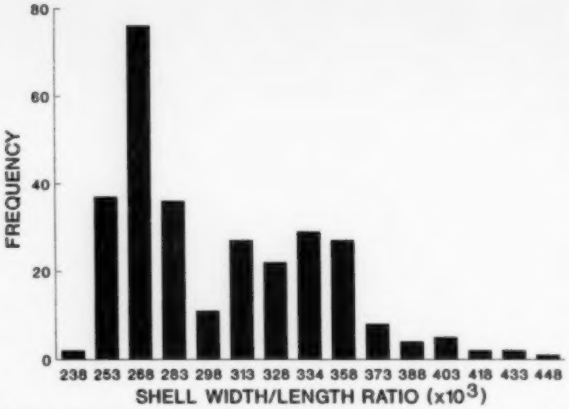

FIG. 4. Frequency distribution of shell width to length (mm) ratios for all *M. deauratum.*

the western portion of the north shore of the Gulf of St. Lawrence and then only in the immediate subtidal zone (Merrill et al. 1978). The species does not appear to be entirely restricted to that area, however. Small individuals of the species have been sampled in a shallow coastal area (Petpeswick Harbour) of Nova Scotia (D. Davis, Nova Scotia Museum) and scattered on the eastern North American continental shelf. Records we have found include individual specimens on Georges, Roseway, Emerald, Western (Massachusetts), and Banquereau banks and as deep as 329 m off Banquereau Bank (Harvard Museum of Comparative Zoology, No. 63578, examined by M.S.H.). Eight of the 10 samples in that collection were offshore records. All the deep specimens in the Harvard collection are similar in size to the smaller specimens sampled in the present study. A mid-sized specimen from the Grand Banks is also present in that collection. Despite these observations, the population on Southeast Shoal is the most easterly recorded and the only record of living individuals of maximal size known outside the Gulf of St. Lawrence.

In addition to the observations by Nesis (1965) of *M. arctatum*, four living specimens of *M. arctatum* was sampled in Canadian fisheries surveys on the northern tip of the Southeast Shoal (43°50′N, 50°5′W, 29 fathoms, Allen (1965)). We confirmed Allen's identification by reexamining the same specimens (holdings of Huntsman Marine Science Centre, St. Andrew's, N.B., Cat. No. ARC9359506). These were noted by Allen to resemble the specimens for the species in Gould (1870). The shell width to length ratios (0.41 and 0.44) of two of these individuals were at the extreme right of the width/length frequency distribution for the *M. deauratum* in our study (Fig. 4). The length to height ratios of 1.43 and 1.52 for these individuals were below the lower 95th percent confidence interval for the mean length/height ratio (1.65 ± 0.008) for our data set. Both of these observations tend to support those authors' identifications. In contrast, we found abundant shells but no living individuals of the characteristic *M. arctatum* shape. Both *M. deauratum* and *M. arctatum* are usually observed at shallower depths than those on the Grand Banks and in large numbers (Davis 1964, 1965), and both also occur in the Gulf of St. Lawrence (Merrill et al. 1978; Brêthes et al. 1986). Merrill et al.'s (1978) review of the distributions of both of these species, however, made no mention of Nesis's or Allen's findings, and therefore missed the implications of the presence of *Mesodesma* on the Banks.

It is possible that populations of both species are present in the area, or that earlier authors confused the species. Another possibility is that *M. deauratum* is a morphological variant of *M. arctatum* in response to different environmental conditions. We noted differences in shell form between the two size groups of clams in our study, indicating a possible age-specific differential growth in certain dimensions (young clams were more elongate). There are at least two factors that could be responsible for this difference. Growth rates of suspension-feeding bivalves are reduced with increasing density (Woodin 1976). These observations are consistent with the more widely recognized fact that density-dependent intraspecific competition is a regulator of both individual and population growth (Ricklefs 1979). Also, shell form in the soft-shell clam *Mya arenaria* has been shown to be affected by sediment texture (Newell and Hidu 1982), resulting in more globose clams occurring in fine-grained deposits. The spectrum of particle sizes at our sampling station was not particularly wide (Table 1), and therefore the differences we observed are more likely due to crowding than sediment texture.

The recent geological history of the Grand Banks helps to explain the presence of this species in the modern day sublittoral. The Southeast Shoal was above sea level during various glacial advances, the most recent being the Pleistocene–Holocene low sea level stand between 12 and 18 000 yr B.P. The Shoal may not itself have been glaciated, but became submerged following glacial retreat and subsequent sea level rise, and would have been a high-energy surf zone. A contiguous coastline would have linked the area with the Gulf of St. Lawrence where the species also occurs. Fossil *M. arctatum* distributed widely on the continental shelf of the western North Atlantic were probably deposited during the Holocene transgression when the species lived in the advancing surf zone (Merrill et al. 1978). The population of *M. deauratum* on the Southeast Shoal may have originated during this period as a littoral population connected by a contiguous coastline along the Laurentian Channel (the former channel of the St. Lawrence River). Rising sea level could thus have separated the clams here from those in the Gulf of St. Lawrence. Carscadden et al. (1989) have sug-

TABLE 3. Dominant benthic invertebrate species at Station 48 during four samplings in 1980.

May	July	September	November
Crustacea	Crustacea	Crustacea	Crustacea
Balanus crenatus	*Acanthohaustorius spinosus*	*Amphiporeia lawrenciana*	*Acanthohaustorius spinosus*
Amphipoda: Pleustidae	*Anonyx nugax*	*Monoculodes edwardsi*	*Anonyx nugax*
	Phoxocephalus holbolli	*Phoxocephalus holbolli*	Amphipoda: Pleustidae
	Amphipoda: Pleustidae	*Priscillina armata*	*Pontogeneia inermis*
	Priscillina aramata	*Unciola irrorata*	*Unciola irrorata*
Mollusca	Mollusca	Mollusca	
Colus sp.	*Mesodesma deauratum*	*Mesodesma deauratum*	
Mesodesma deauratum			
Modiolus modiolus			
Hiatella arctica			
Polychaeta	Polychaeta	Polychaeta	Polychaeta
Exogone hebes	*Harmothoe imbricata*	*Micronephtys minuta*	*Exogone hebes*
Harmothoe imbricata	*Harmothoe spinulosa*	*Ophelia limacina*	*Glycera capitata*
Nephtys discors	*Pholoe minuta*	*Scolelepis squamata*	*Scolelepis squamata*
Phyllodoce maculata	*Scoloplos acutus*		
		Echinodermata	Echinodermata
		Stereoderma unisemita	*Stereoderma unisemita*

gested that a bottom-spawning population of capelin (*Mallotus villosus*) in the same area originated as a relict of populations that spawned in the surf zone when the Shoal was an island. The blue mussel (*Mytilus edulis*) was found on the Southeast Shoal by Nesis (1965) and may also be relict. Nesis reported it to be one of the world's few sublittoral populations of that species and the only one separated from shore by such a great distance. Our sampling of several offshore sites (Hutcheson et al. 1981) detected *M. edulis* only at Station 48. Additional information on the distribution of *M. edulis* on the Southeast Shoal would be useful in supporting this hypothesis.

As a further note, Dr. T. Rowell (Department of Fisheries and Oceans, Dartmouth, N.S.) sampled a dense concentration of large *Mesodesma* on Banquereau Bank in a single grab during commercial mollusc surveys, but because no animals were saved, the identity of the species cannot be confirmed. Banquereau Bank has a record of glacial exposure similar to the Southeast Shoal and shares a similar alignment although on the opposite side of the Laurentian Channel (Fig. 1). If the population is confirmed for Banquereau Bank, the possibility arises that reproducing populations could exist on other offshore banks off eastern Canada and explain the occasional records of small individuals of the species found at greater depth on and adjacent to the Nova Scotia continental shelf.

The environment on the Southeast Shoal may be conducive to existence of *Mesodesma* species, as it is relatively shallow and is exposed to strong current and wave activity from North Atlantic storms (Carscadden et al. 1989) which could frequently disturb bottom sediments. *Mesodesma deauratum* (and *Mesodesma* species in general) tolerates instability through adaptation for rapid burrowing in high-energy sandy environments (Stanley 1970) and it may have an advantage over other less adaptable bivalves in establishing itself in such a high-energy environment.

Although *M. deauratum* appears to be localized to the vicinity of the Southeast Shoal, our study and other records of *Mesodesma* are not sufficient to describe its distribution there. All specimens (Allen 1965; Nesis 1965; this study) have come from the eastern to northern portions of the Shoal, but sampling coverage in other areas is sparse.

Occurrence of high-density patches of *M. deauratum* is consistent with other observations of this genus (Davis 1965; Stanley 1970; Olivier et al. 1971; Merrill et al. 1978). The patchy dispersion characteristics and size segregation observed have also been noted in *Macoma calcarea* (Curtis and Petersen 1977) and *Cerastoderma edule* (Peres 1982), probably resulting from a failure of larval settlement (Woodin 1976) or adults out-competing younger stages for food through intensive feeding. In addition, the presence of high densities of bivalves appears to be a notable feature of sublittoral continental shelf benthic assemblages, although few other bivalves occur at such high density and biomass. Wigley and Theroux (1981) observed patches of unspecified bivalves having a standing crop greater than 19.3 $\mathrm{kg \cdot m^{-2}}$ in inshore bays and sounds on the middle to outer shelf of southern New England and New York Bight. *Modiolus modiolus* (which contributed to high biomass in one of the grabs at Station 48 in May) occurs on Georges Bank with a biomass of 1.3 $\mathrm{kg \cdot m^{-2}}$ (Wigley 1961) and 3.4–11 $\mathrm{kg \cdot m^{-2}}$ (500–1000 $\mathrm{individuals \cdot m^{-2}}$) at the mouth of the Bay of Fundy (Peer et al. 1980). Shallower waters of the midlittoral zone frequently have bivalve densities equal to or greater than that observed for *M. deauratum* at Station 48. *Donax pulchellus* occurs at up to 20 000$\mathrm{\cdot m^{-2}}$ on the West African coast (Pichon 1967), *D. variabilis* occurs at an average of 7141 and maximum of 60 000$\mathrm{\cdot m^{-2}}$ on Florida beaches (Mikkelsen 1981), and *Mesodesma mactroides* occurs in dense concentrations in the beach zone of Argentina (Olivier et al. 1971). Wet weight standing crops of *M. deauratum* in this study are higher than the maximum value of 4.4 $\mathrm{kg \cdot m^{-2}}$ (*M. arctatum* accounted for 95% of the total biomass of 4.6 $\mathrm{kg \cdot m^{-2}}$) and the 1.5 $\mathrm{kg \cdot m^{-2}}$ average found by Nesis (1965) for the Southeast Shoal. There is no indication of the size of individuals he encountered.

Exceedingly high concentrations of suspension feeders occasionally occur in nature, usually accompanied by high-velocity currents and turbulence which supply abundant organic matter (Wildish and Kristmanson 1979, 1984;

Frechette and Bourget 1985; Frechette et al. 1989). The part of the Southeast Shoal where the *M. deauratum* occurs had the highest relative chlorophyll concentrations and primary production of the entire Grand Banks during the study period (Hollibaugh and Booth 1981). The shallow water depth with likely turbulent currents, high water column primary production, and large bivalve community suggests a relatively direct link between water column production and benthic productivity for this portion of the Grand Banks.

Acknowledgments

We acknowledge the support from Mobil Oil Canada Ltd., Gulf Canada Resources Inc., Petro-Canada Exploration Ltd., Chevron Standard Ltd., and Columbia Gas Development of Canada Ltd. during the initial Grand Banks study conducted by MacLaren Marex Inc. (now MacLaren Plansearch Ltd.). The support and assistance of Dr. P.T.P. Tsui and Ms. Leslie Grattan, Mobil's project managers, are gratefully acknowledged. We thank the following individuals for their interest and advice: Gordon Fader, Don Peer, Larry Coady, and Drs. Derek Davis, Barry Hargrave, Mike Lewis, and Arthur Merrill. Dr. Ruth Turner of Harvard's Museum of Comparative Zoology graciously provided access to their mollusc collection.

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Length-specific Weight as a Measure of Growth Success of Adult Atlantic Herring (*Clupea harengus*)

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Winters, G.H., and J.P. Wheeler. 1994. Length-specific weight as a measure of growth success of adult Atlantic herring (*Clupea harengus*). Can. J. Fish. Aquat. Sci. 51: 1169–1179.

We used length-specific weight (i.e., condition) to evaluate growth success of seven stocks of adult Atlantic herring (*Clupea harengus*) in the Northwest Atlantic. Condition of adult Atlantic herring showed large annual changes as a consequence of abundance-dependent effects. This contradicts the general conclusion that adult herring growth contains little abundance-dependent variation. The published literature, however, is based mainly on traditional growth estimators such as annual length increments which measure only a marginal fraction of annual production whereas condition reflects the seasonal accumulation and depletion of energy and therefore can provide a reliable index of total annual production. We found that annual changes in condition of adult Atlantic herring were only weakly correlated with traditional length-based growth estimates. We concluded that the weak evidence for abundance-dependent growth of adult herring in the literature is a consequence of inappropriate growth estimators. The implication of this finding is that the acquisition of surplus energy by herring can be abundance dependent whereas annual increases in length may not.

Nous avons pris le poids spécifique en proportion de la longueur (c.-à.-d. la condition) pour évaluer le succès de la croissance de sept stocks de harengs atlantiques adultes (*Clupea harengus*) qui vivent dans le secteur nord-ouest de l'Atlantique. À cause d'effets qui sont fonction de l'abondance, la condition des harengs atlantiques adultes a marqué d'amples variations au cours d'une année. Ces résultats vont contre l'opinion généralement admise que les variations de la croissance du hareng adulte dépendent peu de l'abondance de l'espèce. Toutefois, dans les articles parus, les chercheurs ont eu recours principalement à des estimateurs classiques de la croissance comme les incréments annuels d'accroissement en longueur, qui ne mesurent que la fraction à la marge de la production annuelle, tandis que la condition montre l'accumulation et l'épuisement saisonniers de l'énergie et peut constituer, de ce fait, un indice fiable de la production annuelle totale. Nous avons trouvé seulement une faible corrélation entre les changements annuels de condition des harengs atlantiques adultes et les estimateurs classiques de la croissance fondés sur la longueur. Nous sommes parvenus à la conclusion que le choix non judicieux d'estimateurs de la croissance est à l'origine du faible lien observé dans les articles scientifiques entre la croissance du hareng adulte et l'abondance. Cela signifie que l'accumulation d'un surplus d'énergie par le hareng peut dépendre de l'abondance alors que ce n'est peut-être pas le cas de l'allongement annuel.

Received February 26, 1993
Accepted December 9, 1993
(JB821)

Reçu le 26 février 1993
Accepté le 9 décembre 1993

Growth of Atlantic herring (*Clupea harengus*) has traditionally been described using the von Bertalanffy (1934) growth model fit to life history size (most often length) trajectories (e.g., Beverton 1963; Anthony and Waring 1980) or using differential growth models incorporating annual increments in length-at-age (e.g., Iles 1967; Winters et al. 1986). Such models formed the basis of a variety of growth studies which have concluded that density dependence (or more strictly abundance dependence) is the main regulator of juvenile herring growth whereas adult herring growth is relatively unaffected by population abundance change (Iles 1967; Cushing 1981; Sinclair et al. 1982; Doubleday 1985; Winters et al. 1986). This apparent lack of an abundance-dependent effect on adult Atlantic herring growth is surprising in view of their relatively large gonads (Wynne-Edwards 1929; Cushing 1967; McQuinn 1989) which have been shown to be related to population abundance variations (Winters et al. 1993).

The inability to demonstrate abundance-dependent growth in adult herring may be a consequence of how growth has been described. Virtually all studies of adult herring growth use length as a measure of fish size and length increments between years (ages) as a measure of annual growth. In this context, Iles (1984) pointed out that variations in total weight of an individual herring during the year adequately reflect the accumulation and elimination of energy during the seasonal growth cycle but are not necessarily in phase with permanent changes in length from one year to the next. It is also important to remember that growth of Atlantic herring is asymptotic in both length and weight (Beverton 1963; Doubleday 1985) and slows markedly with the onset of maturity. Typically, Atlantic herring do not reach maturity until they have achieved nearly 80% of their terminal length (Beverton 1963). Similarly, Doubleday (1985) has shown that instantaneous growth rates of Atlantic herring in terms of weight-at-age average around 0.10 ± 0.05 and decline rapidly with

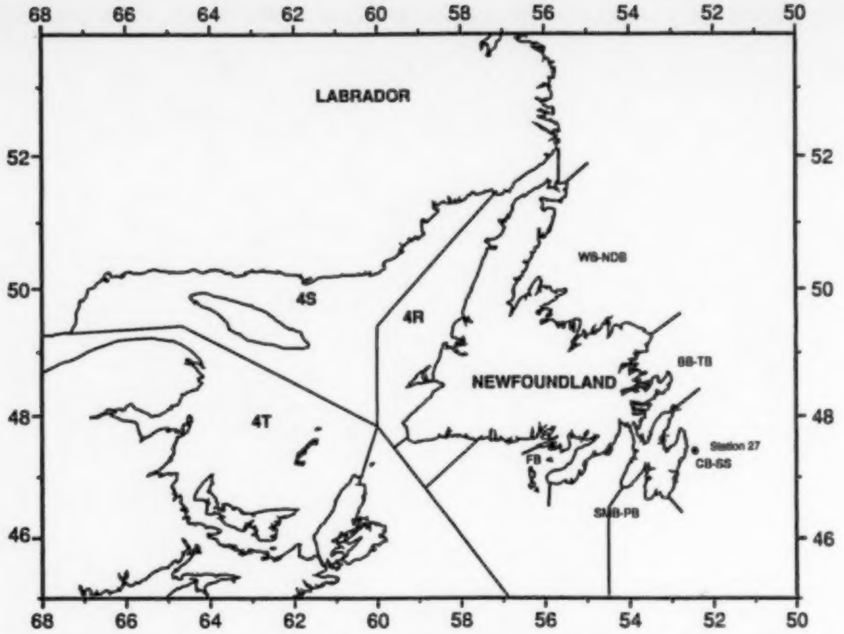

FIG. 1. Map showing localities, Atlantic herring stocks, and place-names mentioned in the text.

TABLE 1. Sample sizes of adult Atlantic herring (number of individuals) by stock area and year for the period 1966–90. All data are on file at the Northwest Atlantic Fisheries Centre, St. John's, Nfld.

						Northern Gulf of St. Lawrence (4R)		Southern Gulf of St. Lawrence (4T)	
Year	WB-NDB (SS)	BB-TB (SS)	CB-SS (SS)	SMB-PB (SS)	FB (SS)	AS	SS	AS	SS
1966	—	—	—	249	161	280	252	704	303
1967	—	—	—	573	516	503	748	2 461	831
1968	—	—	—	1 011	2 116	407	296	3 083	1 210
1969	246	567	137	727	293	174	231	2 939	1 664
1970	1 148	344	294	579	194	454	451	3 506	1 652
1971	1 262	1 361	—	507	416	984	315	3 167	1 111
1972	1 396	656	239	2 130	1 041	837	986	1 679	852
1973	445	69	589	4 451	1 594	1 332	1 983	739	1 057
1974	2 093	1 429	1 415	6 246	1 349	977	1 319	912	655
1975	4 108	2 674	2 511	3 816	665	373	671	958	555
1976	5 526	6 935	3 742	3 751	455	517	1 707	870	612
1977	2 620	4 560	1 846	3 845	326	1 597	2 728	812	617
1978	2 625	3 776	1 618	4 452	584	940	2 665	542	56
1979	3 179	4 729	1 521	4 396	899	1 343	2 672	296	562
1980	3 788	4 789	419	1 809	528	1 978	4 461	78	233
1981	4 195	4 413	—	705	10	1 199	4 842	—	—
1982	2 243	1 856	84	1 610	205	3	457	—	—
1983	2 074	2 690	112	1 048	715	—	—	—	—
1984	3 522	2 384	193	1 122	700	—	—	—	—
1985	2 078	2 210	753	509	815	—	—	—	—
1986	2 713	2 514	976	1 264	1 209	—	—	—	—
1987	3 233	3 440	1 129	1 403	1 306	—	—	—	—
1988	3 735	3 737	1 456	1 545	1 273	—	—	—	—
1989	4 397	3 461	1 165	1 248	1 333	—	—	—	—
1990	2 890	3 122	1 150	1 283	1 143	—	—	—	—
Total	59 516	61 716	21 349	50 279	19 846	13 898	26 784	22 746	11 970

TABLE 2. Statistical output of the multiple slope and common slope weight–length regression models of the GLM procedure of SAS for the various stock/spawning group combinations. Run Nos. 1–9 include month and year as class variables whereas run 10 includes spawning group and stock as additional class variables.

Stock area	Run No.	Model	df	Residual mean square	R^2
WB-NDB (SS)	1	Multiple slope	59 001	0.0069	0.86
		Common slope	59 150	0.0070	0.85
BB-TB (SS)	2	Multiple slope	61 429	0.0064	0.84
		Common slope	61 566	0.0065	0.84
CB-SS (SS)	3	Multiple slope	21 152	0.0054	0.85
		Common slope	21 249	0.0055	0.85
SMB-PB (SS)	4	Multiple slope	47 746	0.0063	0.87
		Common slope	47 856	0.0066	0.86
FB (SS)	5	Multiple slope	16 471	0.0066	0.87
		Common slope	16 559	0.0067	0.87
4R (AS)	6	Multiple slope	7 495	0.0060	0.90
		Common slope	7 557	0.0062	0.89
4R (SS)	7	Multiple slope	18 642	0.0060	0.87
		Common slope	18 709	0.0064	0.86
4T (AS)	8	Multiple slope	22 277	0.0044	0.82
		Common slope	22 334	0.0046	0.81
4T (SS)	9	Multiple slope	11 230	0.0055	0.79
		Common slope	11 286	0.0056	0.79
All stocks (AS + SS)	10	Multiple slope	288 075	0.0097	0.80
		Common slope	288 085	0.0098	0.80

age. Furthermore, herring divert an unusually large proportion of their annual production to gonads (Ware 1980). This fraction increases substantially with size (McQuinn 1989; Bradford 1993) to the extent that annual production of a herring remains fairly stable throughout its adult phase even though somatic growth in length has declined to marginal levels (Iles 1974). Clearly, therefore, adult herring lengths do not reflect surplus energy at all.

In this paper, we investigate length-specific weight, or more specifically body condition, as an alternative biometrical indicator of annual growth success of adult Atlantic herring. We postulate that condition, appropriately measured to account for the seasonal maturation cycle, will provide a reliable index of annual surplus production of adult herring and therefore a better standard with which to evaluate abundance-dependent changes in annual growth. We examined how season (i.e., month), location (i.e., stock), spawning group (i.e., spring spawners or autumn spawners), and year influenced condition of adult herring. In particular, we examined condition to assess whether it is a forced physiological trait (Beverton 1987) and therefore essentially a chemical process or a compensatory trait capable of reflecting and controlling population abundance. Reiterating, we propose that the apparent absence of abundance dependence in adult herring growth is a consequence of inappropriate growth estimators.

Materials and Methods

We used data for herring collected from 1966 to 1990 by the Department of Fisheries and Oceans, Pelagic Research Station, Science Branch, St. John's, Nfld. Samples were taken from seven stock complexes inhabiting the coastal waters of Newfoundland and the Gulf of St. Lawrence (Fig. 1). The Newfoundland populations of herring (White Bay – Notre Dame Bay (Stock WB-NDB), Bonavista Bay – Trinity Bay (Stock BB-TB), Conception Bay – Southern Shore (Stock CB-SS), St. Mary's Bay – Placentia Bay (Stock SMB-PB), and Fortune Bay (Stock FB)) are predominantly spring spawners (SS) (Winters and Wheeler 1987). Northern (4R) and southern Gulf of St. Lawrence (4T) populations contain a variable mixture of both spring spawners and autumn spawners (AS) (Winters and Hodder 1975; Moores and Winters 1984).

Typically, random samples of 50 fish were collected from commercial landings and research catches of herring in the seven stock complexes and processed for a variety of biological data. Commercial landings were predominantly by purse seines and gill nets of mesh size 66.7 mm. Research catches were mainly by gill nets fished in a standard fleet of five nets ranging in mesh size from 50.8 to 76.2 mm. The composite length frequency of herring caught by the research gillnet fleet is very similar to that of the purse seines (Winters and Wheeler 1990) whereas commercial gill nets are size selective (Winters and Wheeler 1990). The potential bias of this selectivity was assessed by comparing results from preliminary analyses with, and without, commercial gillnet samples. No major differences were apparent and we included commercial gillnet samples in all subsequent analyses.

Data recorded routinely for each specimen included total length in millimetres, whole body weight in grams, spawning group, sex, and maturity according to the eight-point maturity scale of ICES (Anonymous 1962). Le Cren (1951) has shown that immature and mature fish have different

TABLE 3. Relevant statistical output of the common slope GLM weight–length regression model including main effects of the class variables (month, year, spawning group, and stock) (**$P \leq 0.01$).

Stock area	Run No.	Slope	Intercept	R^2	Type III Source	df	SS	F value	PR > F
WB-NDB (SS)	1	2.93**	−11.32**	0.84	Loglength	1	1468.51	99999.99	0.00
					Month	11	65.76	780.40	0.00
					Year	21	60.09	373.51	0.00
BB-TB (SS)	2	2.86**	−10.84**	0.83	Loglength	1	1208.57	99999.99	0.00
					Month	10	35.16	500.13	0.00
					Year	21	69.40	470.12	0.00
CB-SS (SS)	3	2.72**	−10.02**	0.83	Loglength	1	232.21	38881.51	0.00
					Month	9	17.62	327.85	0.00
					Year	19	17.11	150.82	0.00
SMB-PB (SS)	4	2.95**	−11.35**	0.85	Loglength	1	1070.37	99999.99	0.00
					Month	11	21.20	273.21	0.00
					Year	24	78.86	465.72	0.00
FB (SS)	5	3.22**	−13.01**	0.87	Loglength	1	604.81	89511.49	0.00
					Month	11	7.66	103.03	0.00
					Year	24	11.86	73.11	0.00
4R (AS)	6	2.76**	−10.42**	0.88	Loglength	1	415.06	49665.11	0.00
					Month	11	83.71	910.58	0.00
					Year	16	32.61	243.84	0.00
4R (SS)	7	3.07**	−12.11**	0.86	Loglength	1	738.42	97144.20	0.00
					Month	11	21.33	255.11	0.00
					Year	16	51.57	424.01	0.00
4T (AS)	8	2.82**	−10.81**	0.81	Loglength	1	344.01	71831.60	0.00
					Month	7	4.83	144.13	0.00
					Year	14	16.86	251.50	0.00
4T (SS)	9	2.85**	−10.77**	0.78	Loglength	1	184.59	31509.14	0.00
					Month	7	4.65	113.32	0.00
					Year	14	10.20	124.42	0.00
All stocks (AS + SS)	10	2.96**	11.46**	0.82	Loglength	1	8747.62	99999.99	0.00
					Month	11	189.04	1951.80	0.00
					Year	24	375.47	1776.77	0.00
					Spawning group	1	140.98	16011.32	0.00
					Stock	6	51.10	967.33	0.00

growth stanzas, which is consistent with the effects of the onset of maturity on growth patterns of a wide variety of species (Frost 1945). Accordingly, we restricted our analyses to mature fish, i.e., herring in maturity stages 3–8 and at least 300 mm in total length. Table 1 gives sample sizes and distribution.

Le Cren (1951) and more recently Cone (1989, 1990) described the statistical problems inherent in the use of traditional condition indices. We accept the recommendation of Cone (1989, 1990) that fish condition should be investigated by ordinary least squares parameters from weight–length regression analyses, i.e., condition is defined as variation in the whole weight (soma plus gonads) of herring of the same total length, after testing for differences in slope (form). We analyzed the data using the general linear model (GLM) procedure of SAS (SAS Institute Inc., Cary, N.C.). SAS recommends the GLM procedures as being an efficient method of processing data in unbalanced situations, i.e., where there are unequal numbers of observations for the different combinations of class variables, as is the case with these data. Body weight at a common length was estimated from the following general linear model (log transformed):

$$(1)\quad Y = \mu + A_a + B_b + C_c + D_d + bX$$

where Y is the response variable (i.e., $\log_e$ body weight), X is the continuous covariate (i.e., $\log_e$ total length), and A_a, B_b, C_c, and D_d are class variable effects (month, year, spawning group, and stock, respectively), i.e., equation (1) assumes that herring condition is a multiplicative function of various class variable effects. Initial analyses concentrated on differences in form, i.e., common slope (b) or multiple slope (b_{ab}). We tested for differences in form within stocks and spawning groups (spring spawners and autumn spawners), between spawning groups, and finally between stocks. If a common slope model was appropriate, intercept (μ) differences were then tested based on class variable effects. Finally, we adjusted mean weights to the overall mean length.

Multivariate analyses were initially performed for each herring stock to determine the best correlates of annual condition variation during the period 1966–90. We used the maximum R^2 improvement technique of multiple regression analysis (SAS Institute Inc. 1985, version 5 edition) in con-

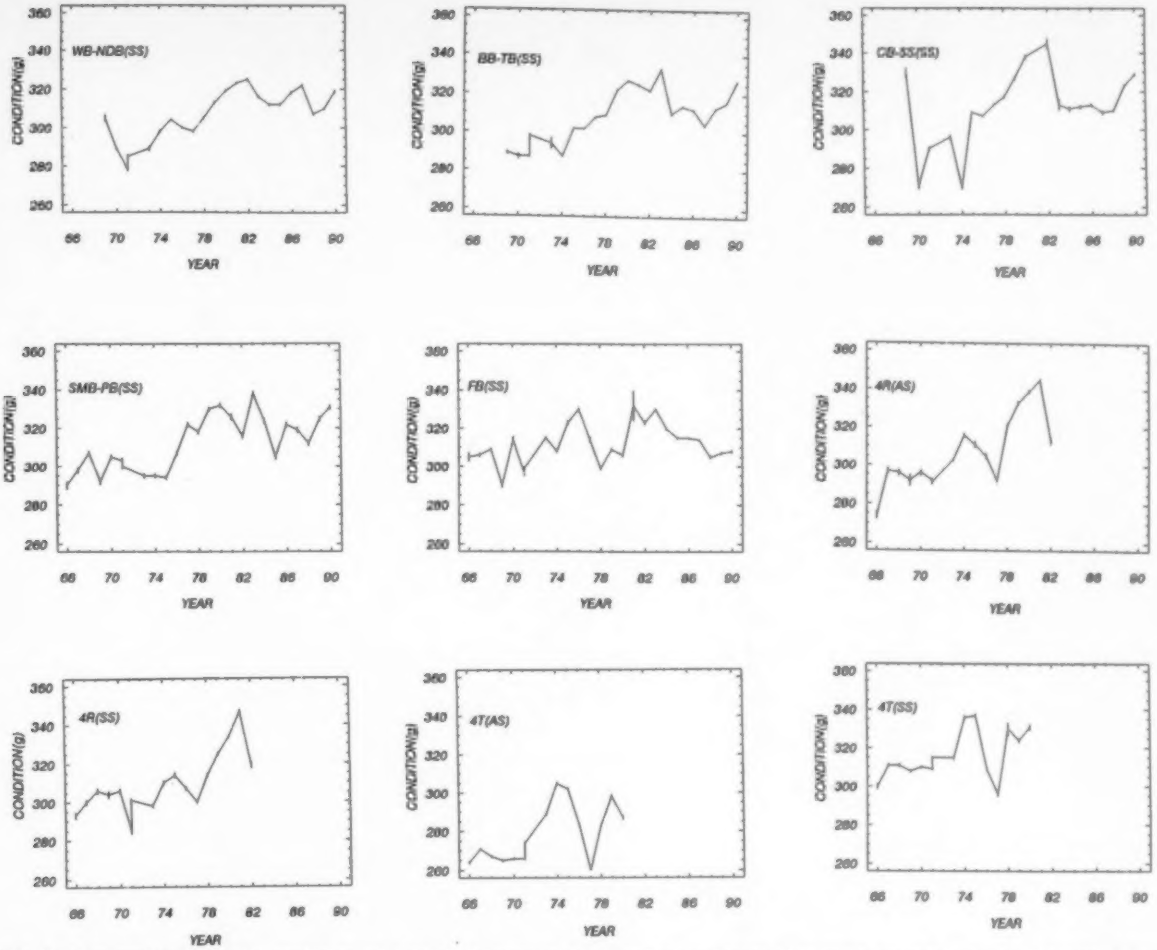

FIG. 2. Temporal variation in condition of Atlantic herring at the grand mean length (341 mm) according to stock (vertical bars represent ±1 SE).

junction with Sokal and Rohlf's (1981) *F*-test to evaluate the significance of increases in R^2 resulting from adding new independent variables.

We examined temperature effects on interannual variations in condition using data from Station 27 (47°31′50″N, 52°35′10″W) off St. John's, Nfld. (Fig. 1) (Akenhead (1983) and data on file at the Northwest Atlantic Fisheries Centre, St. John's, Nfld.). Myers et al. (1990) and Petrie et al. (1992) have concluded that ocean climate signals are highly correlated over the entire Newfoundland Shelf and are well represented by Station 27 measurements. We calculated mean temperature for 0–100 m depth because there are no significant herring concentrations deeper than 100 m in Newfoundland coastal waters (Wheeler et al. 1989). The temperature permutations considered were quarterly sums which approximately matched the seasonal physiological cycles associated with overwintering (January–March), spring feeding and spawning (spring spawners) (April–June), summer feeding and spawning (autumn spawners) (July–September), and the fall feeding period (October–December).

We tested the effect of population abundance (Bioindex) on interannual variations in condition using stock-specific biomass estimates (ages 2+). These were normalized to the year 1972 using data given in Winters and Hodder (1975), Ahrens (1985), Wheeler et al. (1985, 1991), McQuinn (1986),

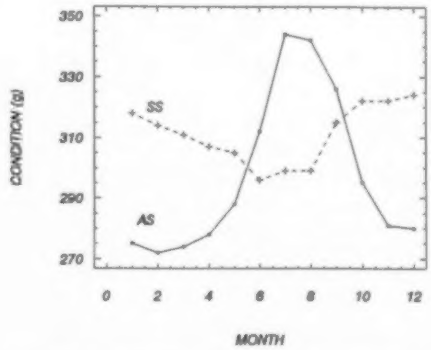

FIG. 3. Monthly variation in condition of Atlantic herring at the grand mean length according to spawning group (SE's too small to plot).

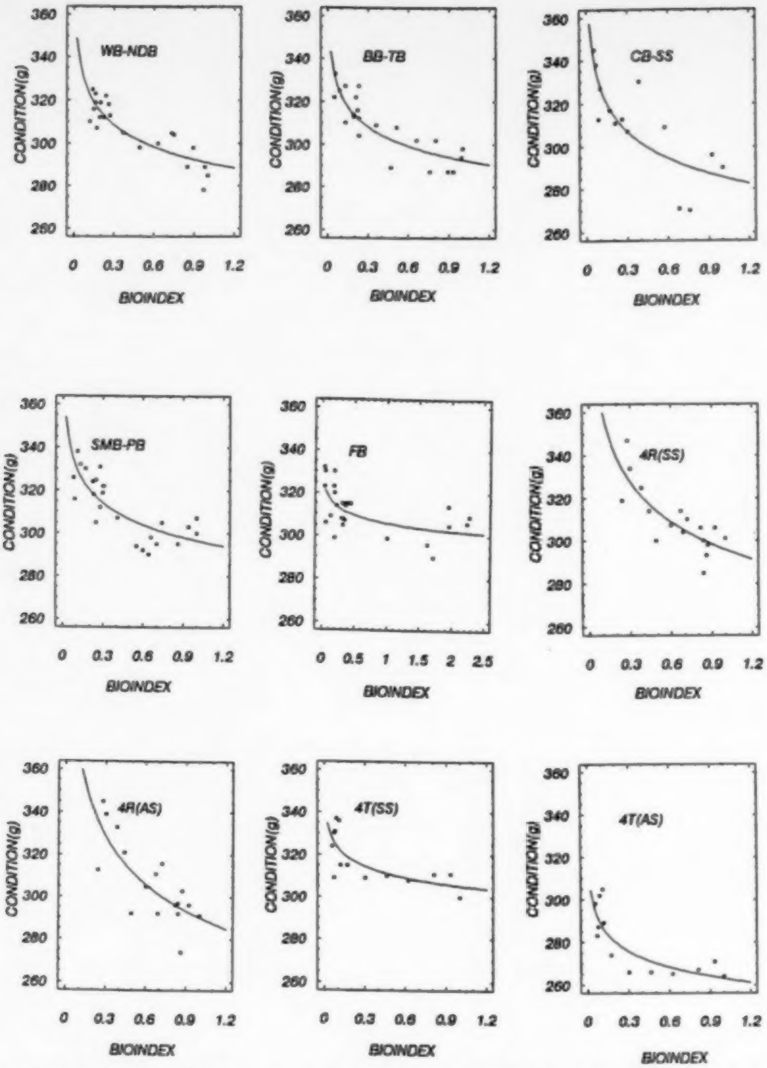

FIG. 4. Relationships between annual condition and population abundance (Bioindex) as described by the multiplicative model for each Atlantic herring stock (see text for details).

TABLE 4. GLM estimates of condition at the grand mean length (341 mm) for each of the various stocks. The group means are standardized for month effects and year effects.

Stock	Condition ± SE (g)
WB-NDB (SS)	306 ± 0.1
BB-TB (SS)	309 ± 0.1
CB-SS (SS)	316 ± 0.2
SMB-PB (SS)	316 ± 0.1
FB (SS)	313 ± 0.2
Northern Gulf (4R) (SS)	317 ± 0.2
Northern Gulf (4R) (AS)	305 + 0.2
Southern Gulf (4T) (SS)	321 ± 0.3
Southern Gulf (4T) (AS)	297 ± 0.1

Winters et al. (1986), and Chadwick and Cairns (1988). The year 1972 was chosen as the standard because maximum biomass levels were observed then for most of the stocks.

Results

Selection of the Appropriate Model

We found negligible reductions in mean square error and improvements in R^2 when fitting multiple or common slopes to weight–length regressions for each stock (runs Nos. 1–9, Table 2), i.e., there are no significant effects of month and year on the slopes. Therefore, we accepted the common slope model for each stock. Results for run No. 10 (Table 2) show that there was only a small reduction in the mean square error and a negligible increase in the R^2 level when separate slopes were fitted to each stock and spawning group. Therefore the common slope model is adequate for all combinations of class variables (month, year, spawning group, and stock area) and condition can be compared across the various subgroups free of the potential complications of differences in form. We then tested for intercept differences due to class variable effects within stocks and spawning groups, and for all stocks combined (Table 3). All class variables were significant, with the year effect being the most important and the stock effect being the least important (Table 3).

Variability in Condition

Interannual variations in condition at the grand mean length were substantial for each herring stock (Fig. 2). Based on the coefficient of variation, condition was most variable for Stock CB-SS (8.4%) and the least variable for Stock FB (3.5%). Temporal patterns differed among stocks. In general, condition for east coast Newfoundland herring stocks (WB-NDB to CB-SS) increased from the late 1960's to the early 1980's and declined subsequently. Condition of Stock FB herring increased in the late 1960's to the mid-1970's. After, it fluctuated randomly until the early 1980's and then declined. Condition for the northern Gulf of St. Lawrence (4R) herring stock increased from the late 1960's through to the early 1980's for both spawning groups. In the southern Gulf (4T), condition for both spawning groups increased to the mid-1970's and fluctuated randomly until 1980, the last year for which data exist.

Monthly variations in herring condition were also substantial (Fig. 3). They were greater in autumn spawners (range = 280–343 g; CV = 8%) than in spring spawners (range 290–323 g; CV = 3%). In addition the monthly variation of the two spawning groups varied inversely. In spring spawners, seasonal condition remained at the late autumn peak until early winter. It declined until June when spawning was completed. This was followed by a rapid rebuilding of condition in late summer. In autumn spawners, condition peaked for a short period in midsummer. It then declined rapidly, after spawning began in September, and remained low until late spring. At the grand mean length, spring spawners were on average significantly ($P < 0.01$) heavier than autumn spawners (314 versus 299 g).

Spatial variation in condition, according to stock, was less than the variation by spawning group, month, or year (range 289–311 g; CV = 2%) (Table 4). Condition of Atlantic herring was lowest along eastern Newfoundland and highest in the southern gulf of St. Lawrence spring spawners.

Patterns of Condition Variation

Condition and abundance

For each stock, and for all stocks combined, the best fit between annual condition (LSMean) and population abundance (Bioindex) was achieved using a multiplicative model (Fig. 4) as follows (asterisks: 1977 data point removed):

Stock code	Model	R^2	*P* value
WB-NDB (SS)	LSMean = 283 Bioindex$^{-0.05}$	0.73	<0.01
BB-TB (SS)	LSMean = 288 Bioindex$^{-0.04}$	0.73	<0.01
CB-SS (SS)	LSMean = 262 Bioindex$^{-0.07}$	0.67	<0.01
SMB-PB (SS)	LSMean = 287 Bioindex$^{-0.05}$	0.64	<0.01
FB (SS)	LSMean = 282 Bioindex$^{-0.02}$	0.44	<0.01
4R (SS)	LSMean = 311 Bioindex$^{-0.08}$	0.66	<0.01
4R (AS)	LSMean = 355 Bioindex$^{-0.09}$	0.60	<0.01
4T (SS)	LSMean = 289 Bioindex$^{-0.02}$	0.31	0.03
4T (SS)	LSMean = 288 Bioindex$^{-0.03}$	0.52*	<0.01
4T (AS)	LSMean = 273 Bioindex$^{-0.03}$	0.45	<0.01
4T (AS)	LSMean = 273 Bioindex$^{-0.04}$	0.66*	<0.01
All stocks	LSMean = 295 Bioindex$^{-0.04}$	0.78	<0.01

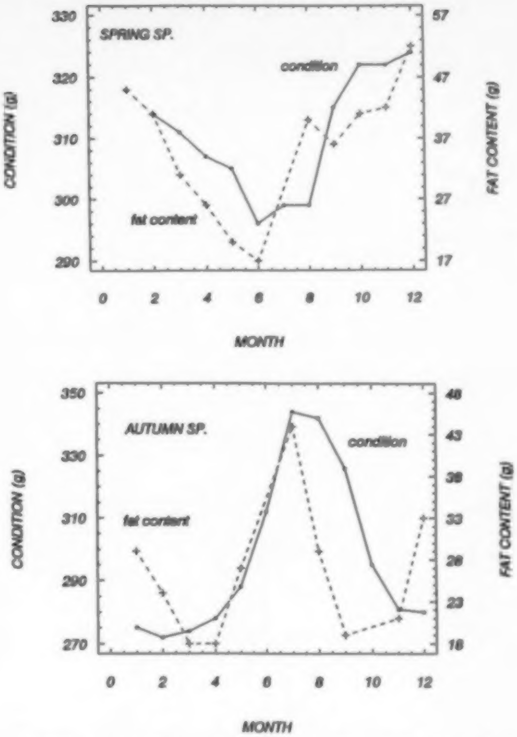

FIG. 5. Relationship between seasonal condition of Atlantic herring and fat content for spring spawners (top panel) and autumn spawners (bottom panel) (fat content data from Hodder et al. 1973).

Fits of the multiplicative model were significant for all stocks. For the southern Gulf (4T) herring population, however, a much better fit was obtained when the apparently anomalous 1977 data point was removed. In that year, substantial numbers of "pygmy" herring normally found in the St. Lawrence estuary area (Jean 1956) occurred in samples of herring from the traditional spring fishery along the western "edge" of Cabot Strait.

The addition of temperature as an independent variable with population abundance in multiple regression analysis failed to significantly increase R^2 levels based on Sokal and Rohlf's (1981) *F*-test.

Condition and lipid content

Various authors (e.g., McGurk et al. 1980; Blaxter and Hunter 1982) reported that the seasonal cycle of accumulation and depletion of energy reserves of Atlantic herring reflected lipid content changes. We tested this using lipid

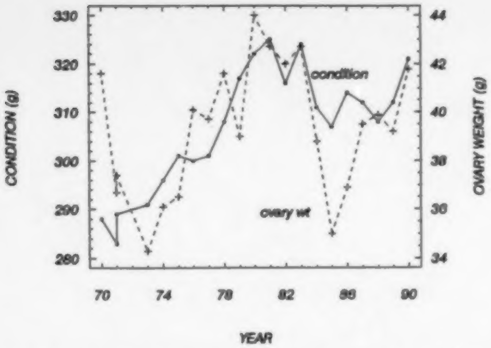

FIG. 6. Relationship between annual condition of Atlantic herring and ovary weights (see text for details).

content data from Hodder et al. (1973) for herring in the Newfoundland area. These data were expressed as a percentage of whole body weight. Iles (1984) showed that such relative lipid content data do not necessarily reflect changes in absolute lipid levels because other proximate components also vary with time. We converted the relative lipid content data in Hodder et al. (1973) to absolute levels for each spawning group and month using monthly body weights (at the grand mean length) derived in this study (see Fig. 3). Lipid content and condition were positively correlated (r = 0.73, $P < 0.01$) for spring spawners (Fig. 5). The summer peak in condition for autumn spawners (Fig. 5) coincided with high lipid content but the rapid rebuilding of lipid reserves in late fall was not reflected by a similar improvement in body condition. Consequently, the relationship between seasonal condition and lipid content was not significant ($r = 0.49$, $P = 0.15$) for autumn spawners. The average annual fat content of spring spawners (36 ± 3.3 g) was significantly higher ($P = 0.03$) than that of fall spawners (26 ± 2.6 g), consistent with the higher average condition of spring spawners.

Condition and reproductive output

Atlantic herring have large gonads which have been shown to vary in size on an annual basis (Winters et al. 1993). We tested the relationship between condition and reproductive output (ovary weights) of spring-spawning herring in the Newfoundland area for the period 1970–90 (Winters et al. 1993). Ovary weights were positively correlated with interannual variations in condition of Atlantic herring during the period 1970–90 ($r = 0.60$, $P < 0.01$) (Fig. 6).

Condition and interannual growth increments

We tested the relationship between condition and annual length increments expressed in terms of the relative growth coefficient (RGC) (Iles 1967) using data for SMB-PB herring (Winters et al. 1986, table 10). The relationship (Fig. 7) was not significant ($r = 0.29$, $P = 0.37$). We conclude that length increments do not adequately reflect annual growth success of adult Atlantic herring.

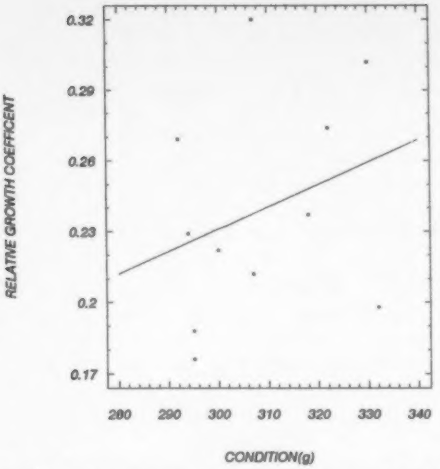

FIG. 7. Relationship between annual condition of SMB-PB herring and relative annual growth (RGC) expressed in terms of length (relative annual growth data from Winters et al. 1986, table 10).

Discussion and Conclusions

This study is the first comprehensive analysis of condition as a measure of annual growth success of adult Atlantic herring. Month and year had the greatest influences on condition. There were also spawning group effects and spatial (i.e., stock) effects. The monthly change in condition of spring spawners was smaller than for autumn spawners, but was closely linked with lipid content changes. This seasonal synchronicity was not as closely linked in autumn spawners.

Condition of Atlantic herring was a nonlinear function of abundance for all stocks. Thus, changes in abundance at low levels were associated with greater changes in condition than when corresponding abundance changes occurred at high stock levels. Condition was only weakly reflected in the traditional length increment measures of growth but was significantly correlated with annual changes in total reproductive output.

Differences in the level of seasonal variability in condition of autumn spawners versus spring spawners reflect what is known about differences in the annual cycle of acquisition and depletion of energy reserves. Bradford (1991, 1993) reported that at full maturity, autumn-spawning herring, which have a brief maturation period (Hodder et al. 1972; McQuinn 1989), are in better physiological condition than spring spawners, which have a long maturation period. Autumn spawners divert more energy to gonad production than spring spawners (Bradford 1991, 1993), hence their larger gonads and corresponding better condition at spawning. It follows that because of their larger reproductive loss, autumn spawners have a much greater decrease in condition than spring spawners after spawning. Further, autumn spawners have only a short and low-intensity feeding season after spawning (Parsons and Hodder 1975; Messieh et al. 1979). It satisfies overwintering metabolic requirements (Bradford 1991) but is insufficient to improve body condition (Fig. 5, bottom panel). Spring spawners, however, rapidly restore body condition (and lipid content) during the summer feeding season and sustain it during the fall maturation period. Therefore, they begin the overwintering period in peak condition. Spring spawners remain in good condition for longer periods during the year than autumn spawners, hence their better average condition. In this regard, we agree with the conclusion of Bradford (1993) that the use of condition as a common measure of Atlantic herring implies that the fish being compared are at the same point in their seasonal physiological cycle. Comparisons of condition among populations of herring with different physiological cycles (such as spring and fall spawners) should take into account the entire seasonal cycle.

The abundance dependence of condition in adult herring from all seven stocks was surprising given the contrary evidence in the published literature (Shepherd and Cushing 1981; Moores and Winters 1982; Winters et al. 1986). However, this is understandable, given the weak relationship we demonstrated between annual condition and the length-based measures of herring growth, upon which nearly all of the published conclusions are based. The lack of a strong relationship is expected given the asymptotic nature of herring growth (Beverton 1963; Doubleday 1985) and the large proportion of surplus energy which herring populations divert to annual gonad production (Peters 1963; Ware 1980). Condition, appropriately sampled, will reflect this seasonal accumulation and elimination of energy whereas interannual length increments do not. This also explains why abundance-dependent growth has been evident in juvenile herring (Cushing 1981) but not in adult herring. In juvenile herring, only somatic material is produced, and therefore, traditional growth estimators provide a reliable estimate of annual production. This is obviously not the case for mature herring which convert surplus energy progressively more into gonads. These findings are consistent with the possibility, noted by Sinclair et al. (1982) and Ware (1984), that the acquisition of surplus energy may be abundance dependent whereas growth in length is not. In the parlance of Beverton (1987), condition is therefore a compensatory trait whereas growth in length is a forced trait controlled by temperature-dependent chemical processes. Therefore, we recommend that growth estimators, such as condition, which reflect seasonal changes in surplus production, be used to examine abundance-dependent growth effects in marine fish populations in general, and herring populations in particular.

The influence of abundance dependence on condition that we found is likely to be true for most Atlantic herring stocks. This is because electrophoretic studies (Grant 1984; King et al. 1987) suggest that there is little genetic differentiation among Atlantic herring stocks, and therefore, life history traits will be primarily controlled by proximate factors (Jennings and Beverton 1991). For herring, there has been only one explicit analysis of such abundance dependence of condition, i.e., for mature Icelandic summer-spawning herring (Jakobsson and Halldorsson 1984). For this stock, condition factor (Fulton's *K*) was negatively correlated with overall stock abundance. From the literature for North Sea herring, we found a consistent set of length–weight data collected as part of the summer North Sea herring acoustic surveys since 1983 (Bailey et al. 1983; Simmonds et al. 1985, 1986, 1987; Aglen and Simmonds 1988; Kirkegaard et al. 1989; Anonymous 1991). We plotted these data for adult herring of a standard size (29 cm) (Fig. 8). Abundance affects growth of adult herring in the North Sea as well. R.W. Tanasichuk and D.M. Ware (Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., personal communication) reported that biomass and sea temperature influence growth in weight of Pacific herring (*Clupea pallasi*) adults. They also found no influence of abundance on length and concluded that length is an inadequate indicator of adult herring growth. They suggested two reasons for this. First, the nature of weight–length relationships dictates that absolute increases in length and weight are not comparable. For example, a 1-mm increase does not equal a 1-g increase. This becomes more important as the fish become larger. They also found interannual variations in condition. Consequently, an absolute increase in length does not correspond to a specific increase in weight over years. We conclude that abundance dependence of growth is likely to be universal for herring stocks when growth success is expressed in the form of weight-based estimators such as condition.

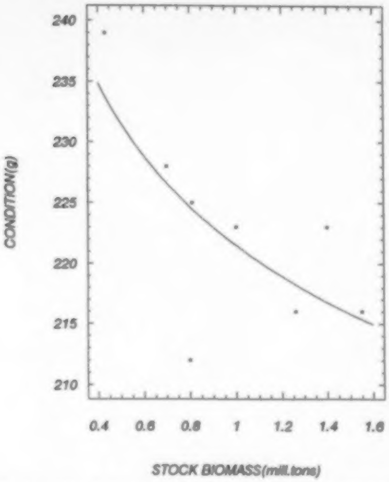

FIG. 8. Relationship between condition of North Sea herring (at 29 cm) and population abundance (see text for data sources).

The nonlinearity in the abundance-dependent acquisition of surplus energy of Atlantic herring is also significant in terms of evolutionary fitness. Ovary weight of Atlantic herring is an exponential function of fish length (McQuinn 1989) and is abundance dependent (Winters et al. 1993). Therefore, when population abundance is low, investment of surplus energy in fish size (and hence its life expectancy and future reproductive output) will be sacrificed for current reproductive needs of the population. These trade-offs in life history traits are consistent with the "cost-benefit" effects expected according to evolutionary theory (Stearns 1976; Calow 1979, 1981; Wooton 1979). This is the expected result because reproduction, as a population-regulating mechanism, operates to increase recruitment at low population levels (Myers and Doyle 1983; Roff 1984; Ware 1984; Jennings and Beverton 1991).

Finally, a variety of experimental studies (Backiel and Le Cren 1967; Weatherly and Gill 1987) have firmly established the connection between intraspecific abundance and fish growth. Our analyses show that abundance dependence is likely to be universal for herring stocks when growth is expressed in the form of condition. There exists therefore a mechanism of population control which could be used as an abundance index for stock assessment studies, particularly those based on calibrated cohort analyses. Length–weight data are commonly collected as part of the commercial sampling process. Therefore, such an index would be inexpensive to maintain and independent of the fishery-based data which are used as major inputs to sequential population analyses.

Acknowledgments

Dr. C. Taggart, Dr. J. Anderson, Dr. R.W. Tanasichuk, and an anonymous referee reviewed various versions of this paper and offered many helpful suggestions which have been incorporated into the text. We also thank the Pelagic Section, Northwest Atlantic Fisheries Centre, St. John's, Nfld., for data collection and collation activities.

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Responses of Plankton, Turbidity, and Macrophytes to Biomanipulation in a Shallow Prairie Lake

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Hanson, M.A., and M.G. Butler. 1994. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. Can. J. Fish. Aquat. Sci. 51: 1180–1188.

We evaluated effects of complete fish kill in a large, shallow, eutrophic lake in Minnesota. Low densitites of *Bosmina* and *Chydorus* ($<100\cdot L^{-1}$) were replaced in the early spring/early summer by high densities of larger *Daphnia galeata* and *D. pulex* ($>100\cdot L^{-1}$) during the first year after the fish kill (1988). During peak daphnid abundance (May–June), chlorophyll *a* concentrations and edible phytoplankton were reduced, water transparency increased, and submerged macrophytes expanded. Orthophosphate and ammonia were detectable during clear-water phases, indicating that phytoplankton were not severely nutrient limited. Increased water transparency in subsequent years (1989–90) apparently was related to decreased sediment resuspension and lower algal biomass owing to the expansion of submerged plants. The fish kill invoked a strong initial response that transmitted to the phytoplankton level and increased water clarity. Higher transparency persisted during subsequent years because submerged macrophytes both responded to improved water clarity and subsequently prolonged it. These results support the contention that removal of fish from shallow lakes may invoke "cascading impacts" that enhance water clarity, stimulate macrophytes, and establish a new steady state.

Nous avons évalué les effets de l'hécatombe complète de poisson dans un grand lac eutrophe et peu profond du Minnesota. Les *Bosmina* et *Chydorus* en faible densité ($<100\cdot L^{-1}$) ont été remplacés au printemps et au début de l'été par *Daphnia galeata* et *D. pulex*, de plus grande taille et en plus forte densité ($>100\cdot L^{-1}$) durant la première année qui a suivi l'hécatombe (1988). Durant la période d'abondance de pointe de daphnies (mai–juin), la concentration en chlorophylle *a* et en phytoplancton comestible s'est abaissée, l'eau est devenue plus limpide et les macrophytes submergés ont proliféré. L'orthophosphate et l'ammoniaque étaient détectables en périodes d'eau limpide; cela indique que le phytoplancton n'est pas gravement limité par l'abondance des éléments nutritifs. Apparemment, l'accroissement de la limpidité de l'eau dans les années subséquentes (1989–1990) dépendait en partie d'une remise en suspension moins importante des sédiments et d'une diminution de la biomasse algaire par suite de la prolifération des plantes submergées. L'hécatombe a suscité une forte réaction initiale qui s'est transmise jusqu'au niveau du phytoplancton et s'est manifestée aussi par la limpidité accrue de l'eau. Ce dernier phénomène a persisté pendant les années suivantes, du fait que les macrophytes submergés ont tiré profit de la limpidité accrue de l'eau et ont subséquemment prolongé ce phénomène. Ces résultats viennent appuyer l'hypothèse que l'enlèvement des poissons dans les lacs peu profonds peut causer des « effets en cascade » qui accroissent la limpidité de l'eau, stimulent la croissance des macrophytes et conduisent à un nouvel équilibre stable.

Received April 26, 1993
Accepted November 25, 1993
(JB898)

Reçu le 26 avril 1993
Accepté le 25 novembre 1993

Two decades of aquatic food web manipulation have stimulated a synthetic "trophic cascade" theory (Carpenter et al. 1985) and a lively dialogue over the reliability of "biomanipulation" (sensu Shapiro et al. 1982; Shapiro and Wright 1984) as a lake management tool (Carpenter and Kitchell 1992; DeMelo et al. 1992). Proponents contend that removal of zooplanktivorous fishes will result in increased densities of large herbivorous zooplankton, increased phytoplankton mortality rates, and improved water clarity over considerable time periods (Hrbacek et al. 1961; Henrikson et al. 1980; Shapiro 1980; Shapiro et al. 1982; Shapiro and Wright 1984; Spencer and King 1984; Carpenter et al. 1985, 1987; Carpenter and Kitchell 1988, 1992; Hosper 1989; Vanni et al. 1990). A synthesis from the first biomanipulation conference (Lammens et al. 1990) and other recent reports suggest that shallow, eutrophic lakes may respond most predictably to fish manipulation (Hanson and Butler 1990; McQueen 1990). Yet overall, many results are equivocal, and "trophic cascade" theory and "biomanipulation" approaches remain highly controversial (DeMelo et al. 1992; Persson et al. 1993).

Phytoplankton community structure and biomass remain of interest to lake managers but the responses of these variables are often unpredictable and difficult to interpret owing, in our opinion, to one or more of the following. (1) Few previous studies have been long enough to allow for identification of dominant trends and causal relationships among variables that collectively reflect ecosystem properties (but see Edmondson 1979; Edmondson and Litt 1982; Scavia et al. 1986; Mills et al. 1987; McQueen et al. 1989; review by DeMelo et al. 1992). In addition, whole-lake studies of >5 yr duration are scattered among a range of lake types. (2) In shallow lakes, bioturbation by fish may influence turbidity, nutrient regeneration from sediments, and phytoplankton biomass (Meijer et al. 1990) but these potential effects are rarely evaluated (McQueen 1990; DeMelo et al. 1992). (3) Nutrient availability is rarely static due to variable loading, regeneration rates, weather patterns, or losses to the hypolimnion (e.g., Shapiro and Wright 1984; Wright and Shapiro 1984; Scavia et al. 1986; Vanni et al. 1990; summary by DeMelo et al. 1992). (4) In shallow lakes, macrophytes may increase dramatically following fish removal and strongly influence phytoplankton biomass and water clarity (McQueen 1990; Hanson and Butler 1990; Lammens et al. 1990; DeMelo et al. 1992). Because macrophytes apparently suppress phytoplankton (Szczepanski 1977; Wiüm-Anderson et al. 1982; McQueen 1990), concurrent increases in both large herbivorous zooplankton and macrophytes confound causal inferences about reductions in algal biomass.

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Shallow lakes may be fruitful ground for biomanipulation tests of "trophic cascade" theory because organisms are not spatially separated by depth and because these lakes afford more static nutrient environments where losses to the hypolimnion are unlikely. However, bioturbation and macrophyte effects are potentially confounding and must be controlled or measured if food web mediated effects at the phytoplankton – water clarity level are to be distinguished from other influences (McQueen 1990; DeMelo et al. 1992).

Here we describe results of complete fish kill in a large, shallow, prairie lake. Fish community structure, plankton characteristics, nutrient dynamics, water clarity patterns, and submerged macrophyte coverage are compared among two or three pretreatment and three posttreatment years. We describe a combination of food web and submerged plant mediated effects that were likely responsible for posttreatment patterns and we discuss implications of these results for shallow lake management.

Materials and Methods

Study Site

Lake Christina is a large, shallow, eutrophic lake located in calcareous till in west-central Minnesota, USA. The surface area is 1619 ha, and the mean depth is 1.5 m with a maximum depth of 4.0 m. Historical accounts indicate that the lake lost nearly all of its previously abundant submerged macrophytes (especially *Potamogeton pectinatus* and *Ruppia maritima* var. *occidentalis*) due to high turbidity in the past two decades. Although once an important waterfowl staging and feeding area, elimination of these food plants greatly reduced the lake's suitability for migrating waterfowl (Hanson and Butler 1994). The lake supported a dense community of planktivorous and benthivorous fishes during the early to mid-1980's. Summer phytoplankton blooms produced chlorophyll *a* concentrations reaching 100 $\mu g \cdot L^{-1}$. Midsummer Secchi disk transparency was typically <30 cm.

Restructuring the Fish Community

In hopes of improving water clarity and stimulating growth of submerged macrophytes, the Minnesota Department of Natural Resources (MDNR) applied 62 700 L of rotenone aerially on 20 and 21 October 1987 to produce a lakewide concentration of approximately 3.0 $mg \cdot L^{-1}$. Black bullhead (*Ameiurus melas*) were caged and observed at various sites around the lake in order to evaluate the extent of the fish kill. These in situ observations and extensive test netting immediately after the treatment indicated that no fish survived.

Largemouth bass (*Micropterus salmoides*) and walleye (*Stizostedion vitreum*) were stocked each year during 1988–90 by the MDNR in an effort to establish a sizable piscivore community and a higher piscivore to planktivore and benthivore ratio. To track changes in the fish community, at least 10 (range 10–27) trap and 2 (range 2–6) experimental gill nets (various mesh sizes) were set in 1982 and during each year from 1985 to 1990. A combination of trap and gill nets was used because passive fish-sampling gears are size and species selective (Hubert 1983). Winter aeration systems were installed at several sites during 1988–89 because the lake has a history of winter oxygen depletion and periodic winter kills.

Light Attenuation, Nutrients, and Plankton

We monitored Secchi disk transparency, vertical light attenuation, and concentrations of major nutrients at a minimum of five locations during open-water periods from 1985 to 1990. Most data reported here were collected during 1986–90 (2 yr before and 3 yr following the fish kill). Water samples were taken at 1-m depth with a Kemmerer sampler and analyzed for total phosphorus, orthophosphate, total nitrogen, and ammonia (Environmental Protection Agency 1974). Vertical light attenuation (Lind 1979) was measured with a Li-Cor model LI 185 quantum meter and a submersible cell. Secchi disk transparency was measured with a 25-cm disk.

Plankton was sampled at least monthly and often biweekly from ice-out in April–October 1986–90 except in 1985, when zooplankton was collected only from June to October. Phytoplankton biomass was estimated from chlorophyll *a* concentration (Strickland and Parsons 1972) in water samples collected as indicated above. During 1986–90, additional water samples collected simultaneously with the chlorophyll *a* samples were preserved in Lugols iodine and phytoplankton was later counted on cleared membrane filters (Lind 1979). Zooplankton was usually collected at 10 sites with an integrated column sampler (Swanson 1978) and preserved in 5% sugar–Formalin solution (Haney and Hall 1973). Pooled lakewide density estimates for *Daphnia* based on these 10 sites produced SE's that typically ranged from 15 to 50 and from 10 to 30% of the mean before and after the fish kill, respectively. During 1986 and 1987, when small-bodied cladocerans and rotifers predominated, samples were concentrated, placed in a Sedgewick–Rafter chamber, and counted under a compound microscope. The abundance of large-bodied daphnids in samples taken from 1988 to 1990 necessitated the use of a counting wheel under a stereomicroscope. Zooplankton body length was measured as the distance from the anterior margin of the helmet to the base of the tail spine (to the nearest 0.01 mm) with a digitizing pad, a personal computer, and a stereomicroscope equipped with a camera lucida. Length-specific maximum filtering rates were calculated for *Daphnia* from regressions of Burns (1969). Filtering rates for other Cladocera were estimated with average filtering rates of Haney (1973). Daily

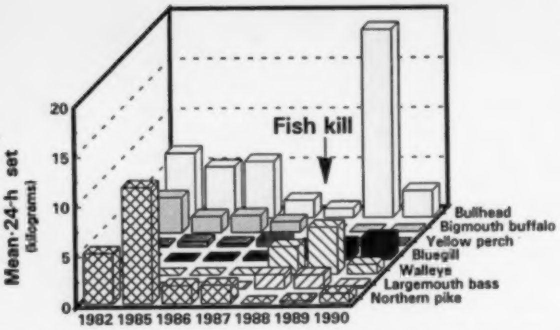

FIG. 1. Mean biomass of most abundant fishes taken in trap nets during 1982 and 1985–90. Vertical bars denote catches of northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion vitreum*), bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), bigmouth buffalo (*Ictiobus cyprinellus*), and bullhead (*Ameiurus*), respectively, front-to-back. Data supplied by the MDNR.

community filtration for Cladocera was estimated monthly by summing filtering rates of dominant taxa.

Submerged Macrophytes

To identify long-term trends, aquatic plants have been surveyed irregularly in Lake Christina since 1947 and each year since 1980 by the MDNR using the methods of Jessen and Lound (1962) and Deppe and Lathrop (1992). At each of a minimum of 35 stations, four samples were taken from the substrate using a weighted plant rake, and frequency of occurrence was calculated, both for each species and for all taxa combined.

Fish Exclosure Experiment

We performed an in situ experiment in 1986 to assess the contribution of bioturbation by fish to turbidity (via sediment resuspension) before the fish kill. Four 3-m-diameter polyethylene limnocorrals, open at the top and bottom, were deployed at a depth of about 1.25 m. Each limnocorral extended from a buoyant hoop above the water surface to a weighted hoop lodged in the sediments (design modified after Landers 1979). Because it is impossible to isolate a water column and exclude fish without some reduction of wave energy, our aim was to test whether water in exclosures would clear with no fish present and slightly reduced wave energy. Protection from heavy winds and floating debris was provided by a 50-m windbreak of wooden snowfence floated on the wind-exposed side of the exclosures. After positioning, rotenone was added to each exclosure ($>10\ \mathrm{mg{\cdot}L^{-1}}$) to ensure that no fish remained. Water samples taken from the center of each exclosure at a depth of 0.5 m were analyzed for percent transmittance using a spectrophotometer (Lind 1979). We tested for associations in transparency between samples taken inside and outside the fish exclosures using correlation analysis (Pearson correlation, SAS Institute, Inc. 1988).

Results

Fish Community Restructuring

Posttreatment observations and test netting indicated that all fish were killed by the rotenone. Bullhead, bigmouth buffalo (*Ictiobus cyprinellus*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*) dominated before the 1987 treatment but overall, fish were somewhat reduced in 1986–87 reflecting partial winterkill (early 1986) and removal during pike salvage efforts (1985–87) (Fig. 1). As expected, the rotenone treatment (1987) and subsequent restocking changed the size and composition of the fish community. Catches of all fish except largemouth bass, walleye (from restocking), bluegill (*Lepomis macrochirus*), and bullhead were low in 1988 relative to pretreatment years (Fig. 1).

Posttreatment stocking of walleye and largemouth bass increased the density of piscivores in relation to planktivores and benthivores (Fig. 1). Black bullhead quickly reinvaded the lake despite preventative weirs and became the most abundant nonpiscivores after the treatment. Bluegill increased over the three posttreatment years, but bigmouth buffalo, probably the most significant pretreatment planktivore, remained absent (Fig. 1).

Patterns of Water Clarity

Water clarity changed markedly after the 1987 fish kill. Pretreatment (1986–87) Secchi disk transparency usually declined quickly after ice-out and remained low (30–40 cm) throughout open-water periods. Vertical light attenuation showed a similar pattern, increasing after ice-out and remaining high (Fig. 2a and 2b). By late May 1988 (after the October 1987 fish kill), we observed increases in Secchi disk transparency and corresponding reductions in vertical light attenuation (Fig. 2c). Higher transparency persisted into June and then diminished (Fig. 2c). Late summer transparency was comparable during 1986–88 (Fig. 2a–2c). High transparency was obvious again during May 1989 (the second posttreatment year), but declined by June (Fig. 2d). Clear water returned by mid-August 1989 and persisted through 1990 with Secchi disk transparency often >1 m during September 1989 to October 1990 (Fig. 2d and 2e). In summary, spring clear-water periods developed during the first two posttreatment years (May–June 1988; May 1989) (Fig. 2c and 2d). Additional improvements in water clarity became obvious in August 1989 and persisted through October 1990 (Fig. 2d and 2e).

Zooplankton and Grazing Rates

Pretreatment samples (1985–87) revealed a very sparse zooplankton community of small-bodied forms. Dominant Cladocera included *Bosmina longirostris*, *Chydorus sphaericus*, and *Diaphanosoma brachyurum* (Fig. 3a). Small *Daphnia galeata* and *D. parvula* (total length <1.0 mm) occurred occasionally. *Cyclops bicuspidatus thomasi* was the most common copepod (Fig. 3b). Common rotifers included *Keratella*, *Polyarthra*, *Asplanchna*, *Testudinella*, *Filinia*, and *Trichocerca*.

Strong shifts in abundance and taxonomic composition of Cladocera were evident following the 1987 fish kill. *Daphnia pulex* and *D. galeata* became predominant zooplankters at all sampling sites by May 1988 and *Daphnia* densities exceeded $100{\cdot}\mathrm{L^{-1}}$ on two dates (Fig. 3a). *Daphnia* remained abundant through June but declined by mid-July and became co-dominant with first *D. brachyurum* and later *B. longirostris*, *C. sphaericus*, and *Ceriodaphnia reticulata*. Spring *Daphnia* abundance followed a similar pattern in

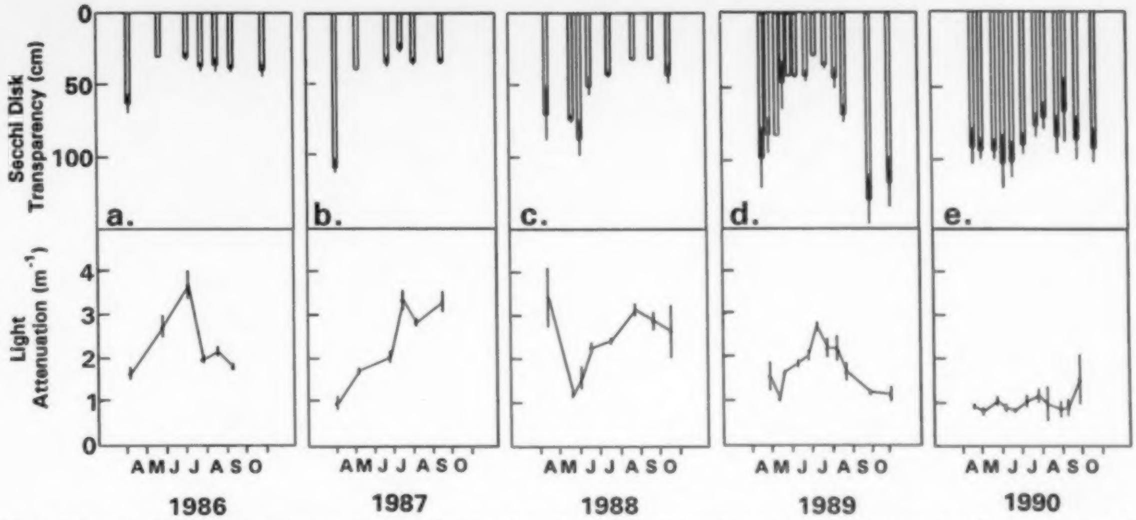

FIG. 2. Mean Secchi disk transparency (vertical bars) and vertical light attenuation coefficient measured with a submarine photometer (solid line) for 1986–90. Vertical lines indicate 1 SE.

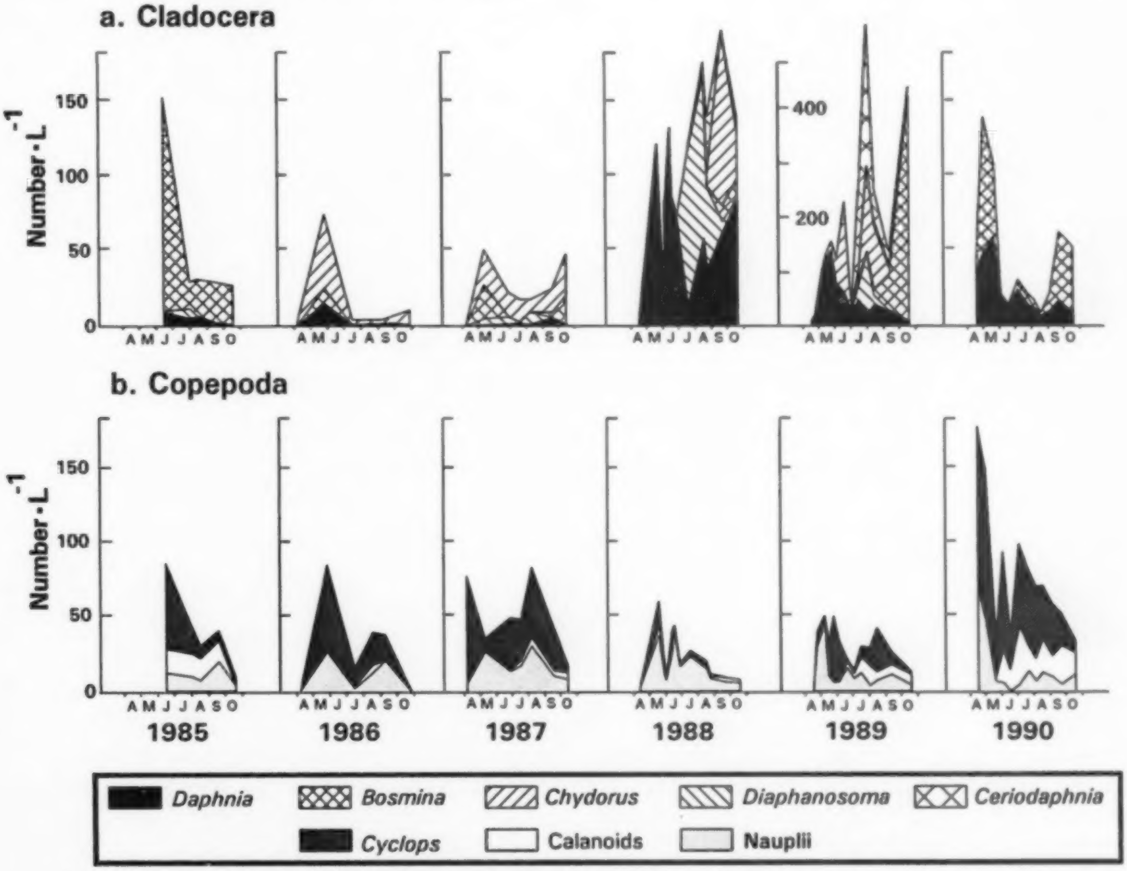

FIG. 3. Mean density of Cladocera and Copepoda during 1985–90. Note that the y-axis scale differs for 1989.

1989 (the second posttreatment year) but quickly gave way to very high densities of *Chydorus*, then *Ceriodaphnia*, and then *Bosmina* during June–October (Fig. 3a). Both the density and diversity of Cladocera were reduced in 1990. A spring pulse of *D. pulex* was apparent, but densities never reached those of the first two posttreatment years (Fig. 3a).

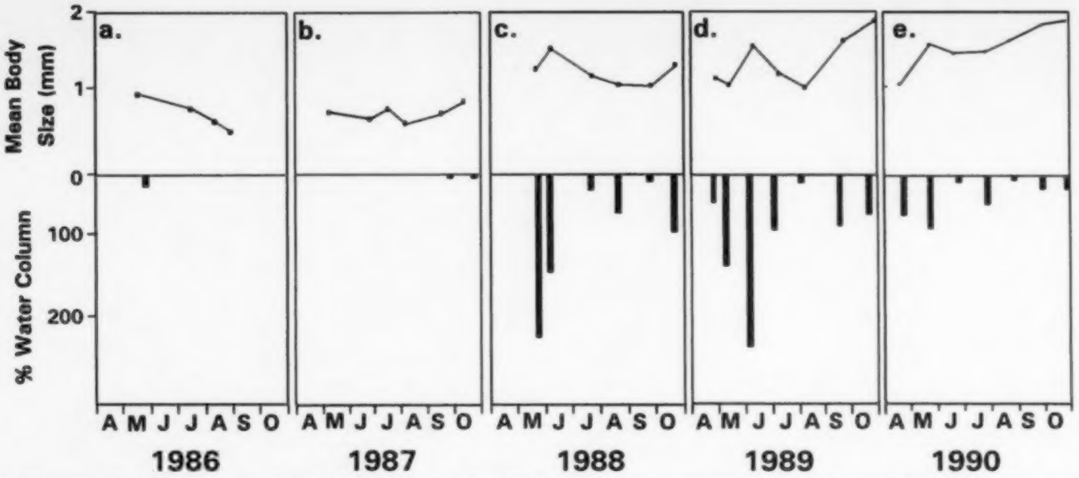

FIG. 4. Mean *Daphnia* body size and daily filtration rates for 1986–90. Filtering rates are based on the relationships of Burns (1969) and Haney (1973).

Overall, copepod abundance and taxonomic composition were not as variable as Cladocera during our study (Fig. 3b). *Cyclops bicuspidatus thomasi* was a notable exception and declined markedly during the first posttreatment year (1988). By 1990, *Cyclops* densities recovered and were often higher than during any previous study years (Fig. 3b).

Changes in zooplankton size structure and filtration rates were associated with shifts in cladoceran species composition. *Daphnia* mean body length (all species combined) increased from <1.0 mm (pretreatment) to >1.0 mm during 1988–90 (posttreatment) (Fig. 4). Peak daily filtration rates increased from <10% of the water column during pretreatment years (Fig. 4a and 4b) to 100–200% during May and June of the first two posttreatment years (Fig. 4c and 4d).

Phytoplankton

Phytoplankton biomass (chlorophyll *a*) and taxonomic composition changed sharply after the fish kill. Pretreatment phytoplankton was dominated by bacillariophytes (especially *Fragilaria* and *Melosira*) and cyanophytes (*Chroococcus*, *Lyngbya*, and *Microcystis*) (Fig. 5b and 5c). Chlorophytes (*Dictyosphaerium*, *Pediastrum*, and *Scenedesmus*) and dinoflagellates (*Ceratium*) occurred at low density. Diatoms were present year-round during the last two pretreatment years and were often dominant (1986) or co-dominant (1987) with blue-greens (Fig. 5b and 5c). Pretreatment chlorophyll *a* peaked at 45–65 $\mu g \cdot L^{-1}$ (Fig. 5a–5c).

Immediately following ice-out in 1988 (the first posttreatment year), an early bloom of diatoms and blue-greens produced chlorophyll *a* concentrations >40 $\mu g \cdot L^{-1}$ in April. By May 1988 (with *Daphnia* density $>100 \cdot L^{-1}$ and daily filtration rates >200%), chlorophyll *a* dropped by >50% and blue-greens largely replaced diatoms. Chlorophyll *a* remained lower through early July but gave way to blue-greens that dominated the phytoplankton through the remainder of 1988 (Fig. 5d). Chlorophyll *a* became comparable with late summer 1986–87 values, but scattered blooms of blue-greens produced extreme variability across the lake from July to September 1988 (Fig. 5d).

During 1989, phytoplankton succession and community structure were comparable with 1988, but biomass differed in that chlorophyll *a* increased after ice-out to a seasonal high >50 $\mu g \cdot L^{-1}$ in mid-May and then declined to <40 $\mu g \cdot L^{-1}$ through October (Fig. 5e). Diatoms were again co-dominant with blue-greens at ice-out but declined by May and remained lower through October (Fig. 5e). Blue-greens predominated from May to October, except for a pulse of *Scenedesmus* in June. In summary, during 1989, phytoplankton shifted quickly away from the edible diatoms to greens and then to blue-greens. Chlorophyll *a* peaked in May and declined, remaining low through October. This contrasts with the 1988 pattern when the spring chlorophyll *a* peak was diatom dominated and late-summer blue-greens produced the highest algal biomass (Fig. 5d and 5e).

Two notable trends were obvious in 1990. First, phytoplankton biomass was sharply reduced relative to other study years. Chlorophyll *a* fell below detection level on 25 May (Fig. 5f) and remained much lower than in other study years (Fig. 6). Second, Cryptophyceae became relatively abundant and numerically dominated the phytoplankton on most dates (Fig. 5f).

Nutrients

Concentrations of phosphorus and nitrogen changed markedly in the first year following the fish kill but were otherwise comparable among years. Total phosphorus and total nitrogen were depressed during May–June 1988 and were generally higher in August and September 1988 than on other dates (Fig. 7), but PO_4^{3-} and NH_3 were usually detectable during April–October 1987–90 (Fig. 7). Exceptions occurred in May and June 1987 (pretreatment) when NH_3 was below the detection limit (0.02 $mg \cdot L^{-1}$) and in April 1990 when PO_4^{3-} was undetectable (<0.005 $mg \cdot L^{-1}$) (Fig. 7). Notably, PO_4^{3-} and NH_3 were above detection levels, and thus probably not severely limiting phytoplankton growth rates during posttreatment clear-water periods (May–June 1988; May 1989, August–October 1989; April–October 1990). Overall, nutrient limitation was probably not very severe before or after the fish kill.

Macrophytes

Historical records indicate that submerged macrophytes

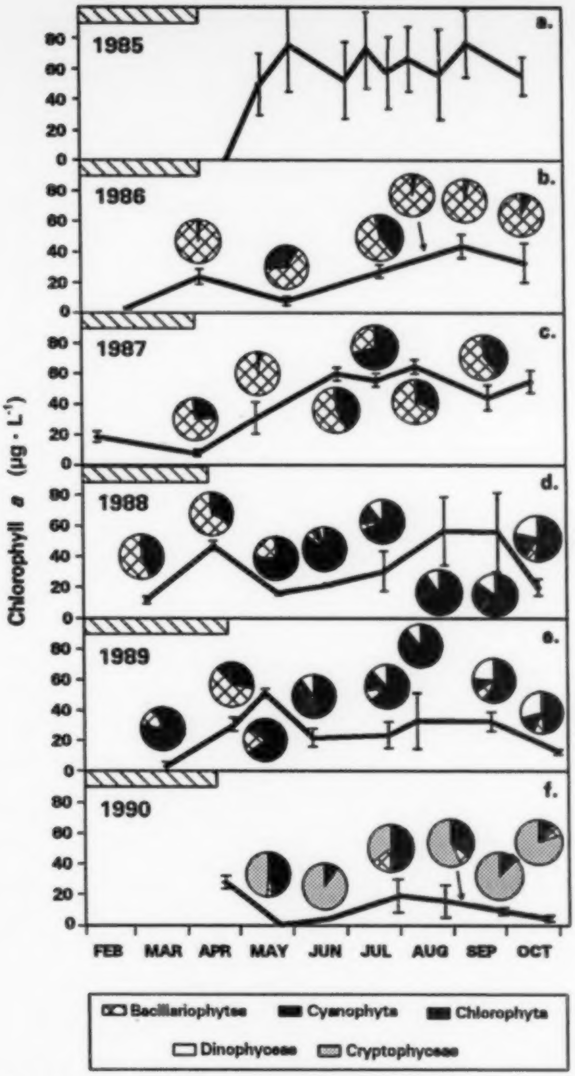

FIG. 5. Phytoplankton biomass (chlorophyll *a*) and general composition during 1985–90. Lines denote chlorophyll *a*. Vertical lines indicate 1 SE. Pies (panels b–f) show community composition at approximately monthly intervals based on mean cell counts at three stations. Hatched areas indicate ice cover.

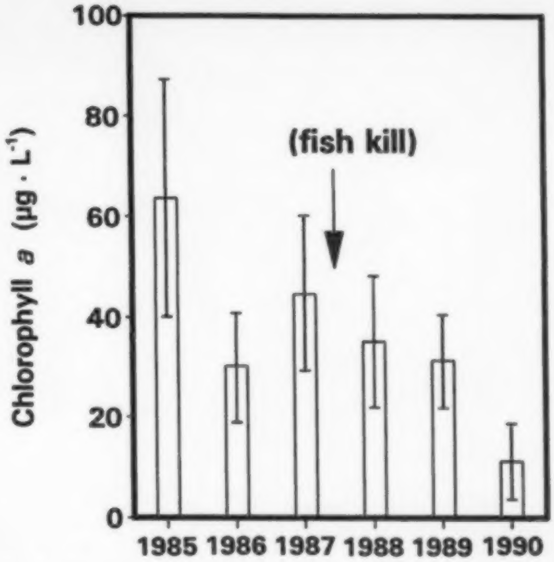

FIG. 6. Mean annual chlorophyll *a* during 1985–90 (open-water periods only). Vertical lines indicate 2 SE.

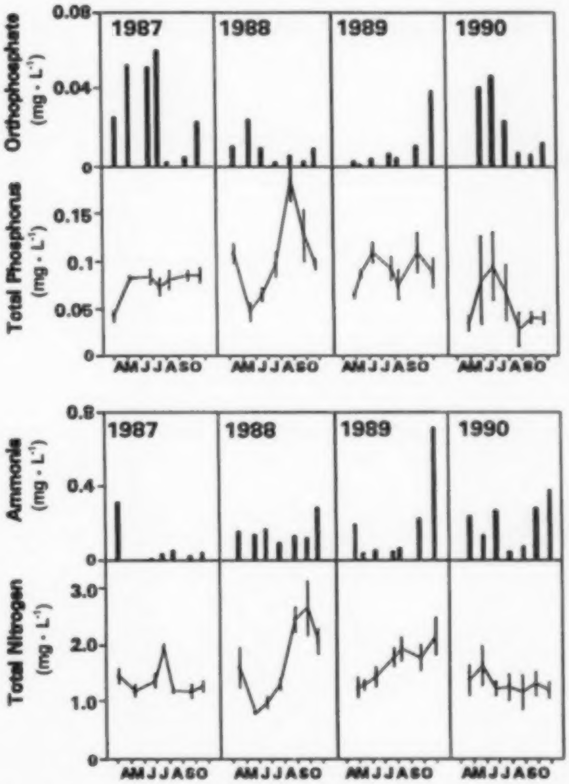

FIG. 7. Phosphorus and nitrogen concentrations during 1987–90. Vertical lines indicate 1 SE.

began a dramatic decline during the mid-1970's (Hanson and Butler 1994). Plants were rare over most of the lake during 1981–86, occurring at <50% of 35 sampling sites. Plants were collected at only 8% of sites sampled in 1985 (Fig. 8). *Myriophyllum exalbescens* and *P. pectinatus* were the only common submergents during the early-mid 1980's (Fig. 8).

After the fish kill, macrophytes were more widely distributed and more diverse than during the previous 8 yr (Fig. 8). *Chara*, *M. exalbescens*, *Najas flexis*, *N. marina*, *R. maritima* var. *occidentalis*, and *P. pectinatus* were abundant following the fish kill (Fig. 8). These sustained increases during 1988–90 appear to signal a departure from the low macrophyte densities of the previous two decades (summarized by Hanson and Butler 1994).

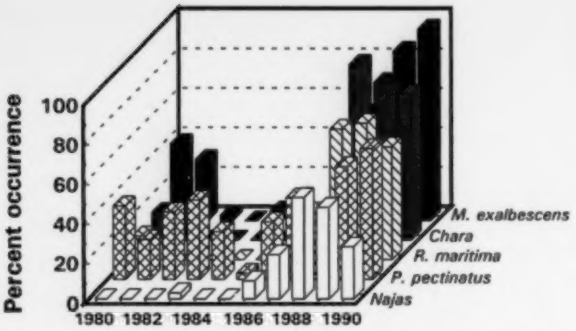

FIG. 8. Results of late-summer plant surveys since 1980. Vertical bars represent percent occurrence of major plant taxa at a minimum of 35 sampling sites. Data supplied by the MDNR.

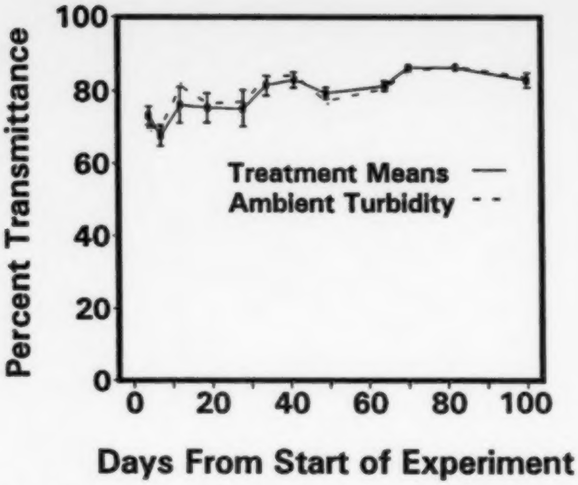

FIG. 9. Transparency inside (solid line, $n = 4$) and outside (broken line) fish-free polyethylene limnocorrals during fish exclosure experiments in 1986. Vertical lines indicate 2 SE for exclosure means.

Sources of Turbidity: Fish Exclosure Experiments

Replicated fish exclosures were maintained for 100 d in 1986. Overall, water clarity in the exclosures did not improve but was highly correlated with ambient water clarity ($r = 0.91$; $p = 0.0001$; Fig. 9). Slight clearing early in the experiment probably resulted from reduced wave energy inside the bags. Bioturbation apparently played no more than a minor role in reducing water clarity prior to the fish kill.

Discussion

We believe our findings help clarify the role of food web mediated responses in shallow lakes for the following reasons. (1) Our treatment was strong and of considerable duration. We assessed abundance and community structure of piscivorous fishes, planktivorous fishes, zooplankton, and phytoplankton for 6 yr (3 yr before and 3 yr following the fish kill). Planktivores were eliminated and subsequently remained at low densities due to the establishment of largemouth bass and walleye. (2) Exclosure experiments indicated that the contribution of bioturbation by fish to turbidity was minor. (3) Nutrients were not strongly limiting during posttreatment clearwater phases. Nutrient reductions (associated with decreased bioturbation or other factors) cannot be credited with posttreatment reductions in chlorophyll *a*. (4) Our data indicate that macrophyte effects were temporally separated from food web mediated effects and results of these separate mechanisms can be distinguished.

Interpretation of unreplicated experiments such as ours is problematic because most statistical procedures are inappropriate. However, replication of large-lake experiments is rarely possible and strong treatments may still produce useful results (Hurlbert 1984). Also, some benefits of replication accrue with careful repetition of similar experiments across a range of systems (Carpenter 1990).

Early Patterns of Water Clarity, Nutrients, and Plankton

We suggest that grazing by *Daphnia* produced spring improvements in water clarity during the first 2 yr following the fish kill (1988 and 1989). Several lines of evidence support our hypothesis. First, replacement of small Cladocera (*Bosmina* and *Chydorus*) with *D. galeata*, *D. pulex*, and *D. schodleri* increased peak daily filtration rates to >200% (Fig. 3 and 4). The latter are comparable with posttreatment rates reported for Round Lake, Minn. (Shapiro and Wright 1984, 100–140%), and Lake Zwemlust, The Netherlands (Gulati 1989, 100–200%). The increase in mean length of *Daphnia* also increased the size range of edible phytoplankton (Burns 1968). Second, nutrient limitation does not explain low chlorophyll *a* during clear-water periods in May–June 1988, August–October 1989, and April–October 1990 because PO_4^{3-} and NH_3 were detectable in our samples (Fig. 7). Third, an increase in *Daphnia* was associated with the replacement of edible diatoms by blue-greens during 1988–89, indicating that grazing largely eliminated edible forms (Fig. 5d and 5e; Lynch and Shapiro 1981; Shapiro et al. 1982; Benndorf et al. 1988). Also, the strong shift to Cryptophyceae in 1990 (Fig. 5f) is similar to trends described by Shapiro and Wright (1984) and Van Donk et al. (1989) with large increases in zooplankton herbivory. Finally, although improved transparency after fish kill sometimes results from reduced bioturbation by fish (Meijer et al. 1990), our fish exclosure experiments indicated that, even at high pretreatment fish densities, bioturbation was not associated with turbidity in Lake Christina (Fig. 9).

Two aspects of our chlorophyll *a* data are enigmatic. First, the 1986 pattern does not resemble that of other pretreatment years. We measured chlorophyll *a* on only one date between ice-out and late July that year and we are unable to explain the low values on that May date or the overall lower levels during 1986 (Fig. 5b and 6). However, historical reports from MDNR lake managers indicate that increasing chlorophyll *a* during May and June 1985 and 1987 (Fig. 5a and 5c) was representative of the typical pretreatment pattern. Second, chlorophyll *a* peaked in May 1989 (Fig. 5e), even with *Daphnia* densities $>100 \cdot L^{-1}$ and filtration rates >100% (Fig. 3 and 4). This peak may have resulted from a rapid shift in the phytoplankton to increased densities of blue-greens and Cryptophyceae during May, allowing higher algal biomass with intense grazing.

Posttreatment Variability in Water Clarity: Role of Macrophytes

Proliferation of submerged macrophytes following planktivore removal from ponds and shallow lakes is well known (Spencer and King 1984; Van Donk et al. 1989; review by McQueen 1990; Meijer et al. 1990). Macrophytes benefit from spring clear-water periods and, once established, suppress phytoplankton through complex interactions involving competition for nutrients, shading, allelopathy, zooplankton refugia, and other mechanisms (Szczepanski 1977; Crawford 1979; Wiüm-Anderson et al. 1982; review by Balls et al. 1989; review by McQueen 1990). When interpreting results of experiments, it may be impossible to identify the primary cause of reduced algal biomass if macrophytes and zooplankton work concomitantly (DeMelo et al. 1992).

Meijer et al. (1989, 1990), Van Donk et al. (1989), and McQueen (1990) described possible transitions from herbivore to macrophyte control of phytoplankton and water clarity in shallow lakes. Our data indicate that herbivory twice invoked spring clear-water phases (1988, 1989) that stimulated rapid expansion of submerged macrophytes. However, extreme water clarity developed during August 1989, persisted through the open-water period in 1990, and during most of that time was associated with relatively low densities of *Daphnia* (Fig. 3a) and reduced filtration rates (Fig. 4e). By August 1989, macrophytes had expanded markedly; *M. exalbescens* was especially dense and was collected at 97% of our sampling sites in 1990 (Fig. 9). These trends support the general contention that effects of biomanipulation in shallow lakes are prolonged by macrophytes (as suggested by Lammens et al. 1990 and McQueen 1990).

Steady-State Considerations and Management Implications for Shallow Lakes

Shallow eutrophic waters are reported to exist in two alternative states, turbid (phytoplankton dominated) and clear (macrophyte dominated) (Scheffer et al. 1993). Shifts between these states appear to be related to levels of planktivory (Timms and Moss 1984; review by Balls et al. 1989). Increased planktivory apparently has the potential to disrupt ecosystem stability and cause rapid replacement of macrophytes by dense phytoplankton communities (Phillips et al. 1978; Balls et al. 1989; Irvine et al. 1989; Scheffer 1989; Stansfield et al. 1989). Feedback mechanisms operate to maintain stability under both clear and turbid conditions (Timms and Moss 1984; Scheffer 1989; Scheffer et al. 1993). These concepts imply a challenge for lake management in that fish manipulations must override feedback mechanisms and "reset" lake ecosystems.

Carpenter and Kitchell (1992) argued that "whole-lake experiments with substantial, sustained manipulations provide the most crucial tests of the trophic cascade hypothesis" and that "we need much more large-scale experimentation before the role of manipulation strength can be evaluated empirically". Persson et al. (1993) reported that pulses of reduced planktivory failed to produce a state shift in a shallow, eutrophic Swedish lake but suggested that more sustained reduction of planktivorous fish might be effective if primary production could be shifted to macrophytes. Our results indicate that planktivore removal has the potential to invoke food web effects that transmit strongly to the phytoplankton – water clarity level in shallow, eutrophic lakes and favor a shift toward a clear-water steady state. While direct food web mediated effects may be short-lived, macrophytes may solve the problem of longevity that still confounds biomanipulation of deeper lakes. In our case, initial clear-water periods were food web mediated and bioturbation was not a major direct or indirect determinant of water clarity or phytoplankton biomass (but see Scheffer et al. 1993). Macrophytes prolonged early effects and appear, at least so far, to impose subsequent constraints on phytoplankton biomass and turbidity. These results support McQueen's (1990) contention that for eutrophic, shallow lakes where macrophytes are tolerable or desirable, food web manipulation is a very effective lake management tool.

Acknowledgements

This research was supported by grants from the U.S. Fish and Wildlife Service (USFWS), the North Dakota Water Resources Research Institute, the Max McGraw Wildlife Foundation, and local sportmen's groups. We especially thank George Swanson, Rey Stendell, Ned Euliss Jr. (USFWS), Robert T. Eberhardt, Tom Carlson, Pat Kirby (MDNR), and the Douglas County Land Corporation for extensive logistical support.

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Predicting the Spatial Distribution of *Dreissena polymorpha* (Zebra Mussel) among Inland Lakes of Wisconsin: Modeling with a GIS

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Koutnik, M.A., and D.K. Padilla. 1994. Predicting the spatial distribution of *Dreissena polymorpha* (zebra mussel) among inland lakes of Wisconsin: modeling with a GIS. Can. J. Fish. Aquat. Sci. 51: 1189–1196.

Previously developed models and available limnological data were used to predict (i) absence or presence, (ii) categorical population density, and (iii) numerical abundance of *Dreissena polymorpha* (zebra mussel) for 194 inland Wisconsin lakes. A geographical information system (GIS) was used to test for associations between predicted lake population density classes and three landscape-scale characteristics (surficial deposits, bedrock type, U.S. Environmental Protection Agency developed ecoregions) that may affect limnological parameters. Although the models used differed in their predictions of specific lakes that would support *Dreissena*, the overall spatial distribution of lakes within a given density class was similar among the models. A significant association was found between each landscape-scale characteristic and *Dreissena* density classes. This study suggests that (1) available lake monitoring data can be used to predict *Dreissena* density for groups of inland lakes, (2) more information on North American lakes with zebra mussel is required to reduce the uncertainty of the models, and (3) spatial analysis using GIS methods can provide valuable insight into the overall patterns of the potential spatial distribution of *Dreissena*.

On a appliqué d'anciens modèles et des données limnologiques à la prévision i) de l'absence ou de la présence, ii) de la densité des populations par catégorie et iii) de l'abondance numérique de *Dreissena polymorpha* (la moule zébrée) dans 194 lacs de l'intérieur du Wisconsin. On a eu recours à un système d'information géographique (SIG) pour voir s'il existe des associations entre les classes de densité de population prévues dans les lacs et trois caractéristiques à l'échelle du paysage (formations superficielles, types de roche en place, régions écologiques de l'U.S. Environmental Protection Agency) qui peuvent influencer des paramètres limnologiques. Même s'ils ne produisaient pas les mêmes listes de lacs dans lesquels on pourrait trouver *Dreissena*, il demeure que les modèles utilisés présentaient sensiblement la même distribution spatiale de lacs pour toute classe donnée de densité. Nous avons trouvé une association significative entre chacune des caractéristiques à l'échelle du paysage et les classes de densité de *Dreissena*. Nos travaux indiquent 1) que les données connues de surveillance des lacs peuvent servir à prévoir la densité de *Dreissena* dans des groupes de lacs intérieurs, 2) qu'il faut recueillir davantage de renseignements sur les lacs d'Amérique du Nord, au regard de la moule zébrée, afin d'abaisser l'incertitude associée aux modèles, et 3) que l'analyse spatiale par des méthodes de SIG peut apporter des renseignements utiles sur les tendances générales de la possible distribution dans l'espace de *Dreissena*.

Received February 5, 1993
Accepted November 26, 1993
(JB783)

Reçu le 5 février 1993
Accepté le 26 novembre 1993

The introduction and establishment of populations of *Dreissena polymorpha* (zebra mussel) in North American lakes, rivers, and reservoirs have been documented over the last 5 yr (Hebert et al. 1989; Nalepa and Schloesser 1993). There has been much discussion of the potential economic and biological impacts of the spread of zebra mussel among the Laurentian Great Lakes (Griffiths et al. 1991; Mackie 1991; Nalepa and Schloesser 1993, and references therein). Also, Carlton (1992) noted that the Great Lakes need to be considered as a source of *Dreissena* for spread to inland lakes. However, less attention has been focused on the questions of how and where *Dreissena* will spread among inland lakes and where they might have important ecological and environmental impacts. For example, with intense development along the shores of many inland lakes, the relative impact on individual property owners could be quite substantial. Also, major power plants are located along larger inland water courses, where biofouling (e.g., clogging of water intake pipes by attaching *Dreissena*) can be a concern. Armor et al. (1993) described four major power plants along rivers in Wisconsin that could be affected, and there are dozens of hydro-power dams located along smaller water courses in Wisconsin and other states and provinces surrounding the Great Lakes. The displacement of native species by *Dreissena*, particularly in protected areas such as the St. Crois River, is an additional concern. The St. Crois River is a rare example of a relatively pristine river in the U.S. upper midwest; invasion of zebra mussel will undoubtedly place rare native species, such as unionid clams, at risk.

The opportunity to examine the potential spread of zebra mussel to inland lakes is timely. *Dreissena* are found in all of the Great Lakes. In Wisconsin, *Dreissena* have been found along the western shore of Lake Michigan, including the southern half of Green Bay, locally along the southern shore of Lake Superior, as well as in the Mississippi River. However, to date, no Wisconsin inland lake has been found to contain *Dreissena* (Wisconsin Sea Grant 1992). Similarly, only a few inland lakes in North America that do not have inflowing hydrologic connections to known *Dreissena* sources have established populations of zebra mussel. These exceptions include Lake Hargus, a reservoir in Ohio (Wisconsin Sea Grant 1992), Lake Wawasee, Indiana (personal observation, 1992), and Eagle Lake, Michigan (Ladd Johnson, personal communication). *Dreissena* populations have also been reported in New York State (New York Sea Grant 1991), but these lakes (Conesus, Seneca, and Cayuga) are likely to have been invaded via waterways connecting to canals from the Great Lakes.

Our study consisted of two parts: (1) we made predictions of potential zebra mussel abundance in a number of Wisconsin lakes (assuming they were invaded) using previously developed models and (2) we used a geographical information system (GIS) to examine landscape-scale characteristics associated with predicted population density levels of zebra mussel in 194 Wisconsin lakes. First, we used three models developed by Ramcharan et al. (1992), based on data from European lakes, to predict *Dreissena* occurrence and abundance in individual lakes. These models are (i) an absence/presence model using discriminant function analysis (DFA), (ii) a categorical density model (absent, low, high population density), also using DFA, and (iii) a numerical, regression-based density model (number per square meter). Hereafter, we refer to these models as the *occurrence*, *density*, and *abundance* models, respectively. We modeled a sample of inland lakes, mapped the spatial distribution of those lakes, and characterized each lake by predicted density class or range, as appropriate for each model. We also compared the results of the three models. Then we associated the population density prediction for each lake with various landscape-scale variables.

Overview of a GIS and Its Application

GIS's are increasingly being used by a broad range of researchers. To date, most GIS usage in aquatic ecology has involved either building geographically referenced databases of ecological data or producing computer-generated maps. These capabilities allow researchers to visualize the spatial relationships among ecological variables and easily perform logical spatial operations. Meanwhile, recent releases of packaged GIS software have taken advantage of window-oriented user interfaces and reductions in hardware costs to make increasingly sophisticated spatial analytical power accessible to the ecological researcher.

GIS will be used most effectively if one takes advantage of what a GIS is designed to do. Lillesand and Kiefer (1987) described a GIS as "a system designed to store, manipulate, and display [geographic] data". A GIS "must be capable of handling both *locational data* and *attribute* or *descriptive* data about features" (italics are the original authors'). A GIS can be differentiated from simple automated mapping by the logical operations that can be performed on sets of spatial features. A set of features is often referred to as a *layer*. A layer consists of the logical combination of the locational and attribute data about like features in an area of study. One such layer might be a set of polygons that represent lake shorelines (locational data), along with their respective limnological data (attribute data). An example of a logical operation is an overlay, which is a logical intersection or union of two or more layers. An example of an overlay process would be a logical union of a wetland layer and a linear road network that might impact the water quality of the wetlands. The resulting GIS dataset could be used to easily analyze the proximity of each wetland to a road. Such an analysis could also easily take into account weighting factors (e.g., traffic level) to account for variance in potential pollutant runoff from a given road. GIS's offer great potential for ecological research, particularly for ecological modeling.

TABLE 1. Summary of data values used to drive the models used in this study. Only values from shallow sampling depths (2 m or less) were used. Concentrations are in $mg \cdot L^{-1}$. nm = not meaningful.

	pH	Calcium	Nitrate	Phosphate
Minimum	5.0	1.0	0.007	0.002
Maximum	9.1	76.2	3.400	0.182
Median	8.0	25.8	0.070	0.005
Standard deviation	nm	16.9	0.398	0.029

In the second part of this study, we used a GIS to perform spatial analysis of the model results from part one, relating them to landscape features associated with a given lake's watershed. Much is known about the relationship between lakes and the characteristics of the watersheds surrounding them (Wetzel 1983). Yet there appear to have been relatively few attempts made to predict water quality variables on such a large scale.

Lake water quality influences can be expected to relate to processes occurring within the entire watershed of a lake. We simplified our study by exploring associations between selected landscape features directly underlying subject lakes, e.g., surficial geology, and the projected *Dreissena* population density of those lakes. We tested the null hypothesis of no association between the predicted density category from the DFA-based density model and two landscape feature attributes for a given lake. We used model-based *Dreissena* predictions and tested for association of predicted lake *Dreissena* status with landscape-scale features.

Additionally, we tested for association between the predicted population densities and ecoregions defined based on lake characteristics. The ecoregions used (Omernik et al. 1988) were developed specifically for lake management purposes. This test was intended to test whether broad ecoregions, refined by lake type clustering, would correlate with predicted patterns of *Dreissena* density. The results of this test could have management implications.

Methods

Modeling *Dreissena* in Individual Lakes

Lake water quality data were obtained from the Wisconsin Department of Natural Resources (WDNR). The source database was the EPA STORET database (U.S. Environmental Protection Agency, Office of Water 1990), which is maintained on a cooperative basis for the state of Wisconsin by WDNR. From this dataset of more than 3000 sampling sites,

TABLE 2. Comparison of *Dreissena* absence and presence predictions among the three models used. For the categorical density model the low- and high-density classes were combined to obtain the present category. For the numerical abundance model, all predictions less than or equal to zero were placed in the absent category, and all predictions greater than zero were placed into the present category. Predictions of abundance less than zero result from absent lakes not being included in the Ramacharan et al. (1992) regression-based abundance model (this model was not forced through the origin).

	Absent	Present	% present
Occurrence (absence/presence)	101	93	47.9
Density (categorical density)	31	163	84.0
Abundance (numerical density)	30	164	84.5

we chose a subset of 194 lakes. Lakes were chosen for the subset when (1) all limnological parameters required by the three *Dreissena* models were available (pH, ionic calcium, nitrate, and phosphate), (2) the size was larger than 8 ha, and (3) the lake was not a reservoir. The 8 ha minimum was chosen because (1) most lakes under 8 ha have not been surveyed and (2) many of these smaller lakes are unnamed, making confirmation of geographic location difficult. For lakes with multiple sampling sites, the site closest to the lake outflow was chosen. From the extensive list of parameters available in the database, only those parameters required to run the three models were extracted.

STORET contains both field and laboratory-processed pH values. When both were available, the values were averaged. Combined nitrate/nitrite, the only available nitrate measure, was used as a surrogate for nitrate alone, since nitrite was expected to be an insignificant contributor to the combined nitrate/nitrite total (Wisconsin State Hygiene Laboratory, personal communication). Similarly, orthophosphate was used as a surrogate for available phosphate, since it was the only measurement available. Sampling history of the lakes varied widely, with samples dating as far back as 1970. Frequency of sampling varied from once every few

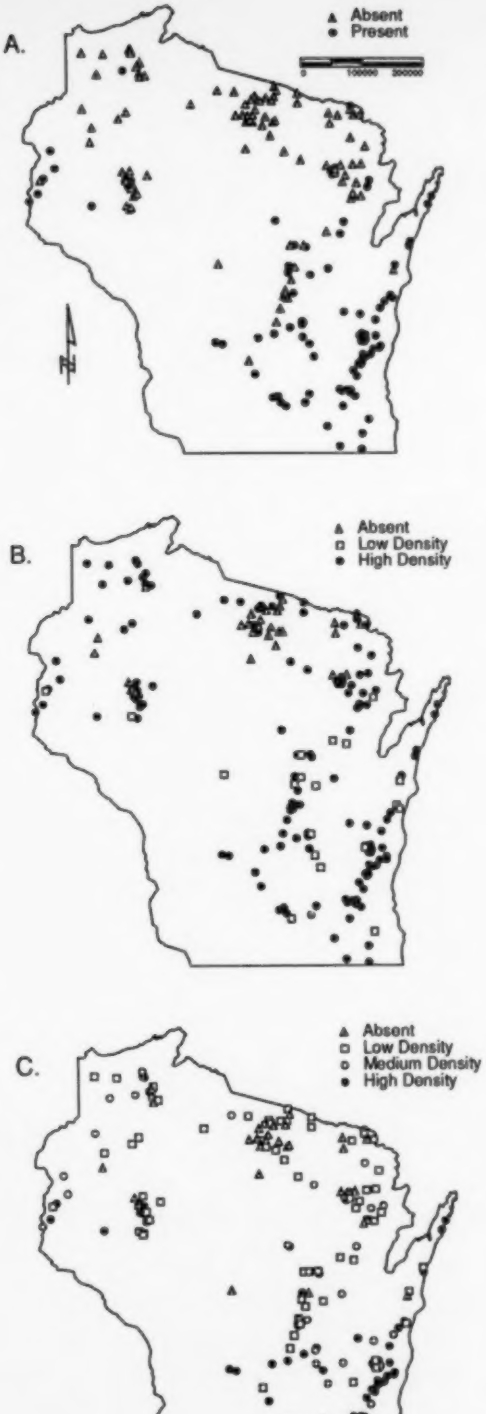
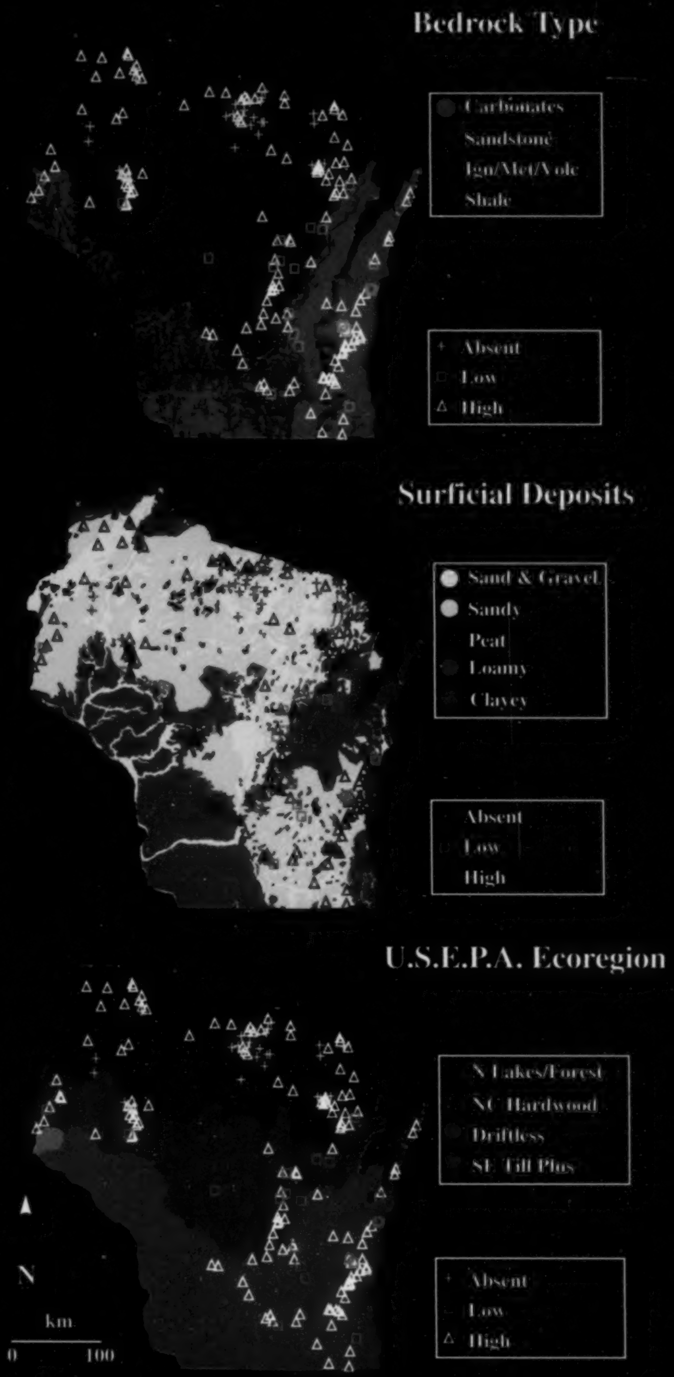


FIG. 1. (A) Map of absence/presence predictions from the DFA-based occurrence model. Open triangles represent lakes where *Dreissena* are predicted to be absent (101 lakes). Solid circles represent lakes where *Dreissena* are predicted to be present (93 lakes). Note that lakes not predicted to have *Dreissena* tend to dominate the north and lakes where *Dreissena* are predicted to occur tend to dominate the southeast. (B) Map of density category predictions based on the DFA-based density model. Open triangles represent lakes where *Dreissena* are predicted to be absent (31 lakes). Open squares represent lakes where *Dreissena* are predicted to be present in low densities (21 lakes). Solid circles represent lakes where *Dreissena* are predicted to be present in high densities (142 lakes). Lakes without *Dreissena* are congregated in the northern area, consistent with Fig. 1A. (C) Map of predictions based on the regression-based abundance model. Open triangles represent lakes with predicted *Dreissena* density of approximately zero or less (52 lakes). The lakes predicted to have *Dreissena* were divided into three equal-sized categories. Open squares represent lakes predicted to have the lowest density, open circles a medium density, and solid circles the highest density. Note that lakes predicted to have the highest *Dreissena* densities tend toward the southeast.


Bedrock Type
Carbonates
Sandstone
Ign/Met/Volc
Shale
+ Absent
□ Low
△ High
Surficial Deposits
Sand & Gravel
Sandy
Peat
Loamy
Clayey
Absent
□ Low
High
U.S.E.P.A. Ecoregion
N Lakes/Forest
NC Hardwood
Driftless
SE Till Plus
+ Absent
□ Low
△ High
N
km
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years to as many as six each year. The majority of lakes had samples taken at various points along a depth profile for a given sampling event. Although *Dreissena* are reported from deep waters, the highest population densities appear to tend toward shallow water. Thus, only data collected at ≤2 m depth were used, as initial colonization is likely to occur in the littoral zone. Within these restrictions, all remaining sample values were averaged across available sampling dates to obtain the final parameters for each lake. Table 1 presents a summary of the final data values.

It should be noted that there were inherent biases in the lake sample data, both temporally and spatially. As noted above, the frequency and timing of the samples varied widely, with many lakes being sampled in only a few closely clustered years. Additionally, many lakes were not sampled as frequently (or at all) in ice-over months. Spatial bias derived primarily from the jurisdictional impetus (i.e., WDNR) for collecting the data. For instance, relatively few sample lakes were located in national forest areas (approximately 600 000 ha in Wisconsin). Further, many of the sample lakes are heavily used for recreation. On balance, this dataset appeared to be the most comprehensive and representative available for Wisconsin, which served the purpose of our study.

We used these data (pH, ionic calcium, nitrate and phosphate levels) in the three models of Ramcharan et al. (1992) to predict zebra mussel populations in each lake. One record for each lake was imported from our database, with the STORET station number as a unique identifier. The records included locational coordinates (latitude/longitude) of the lake's sampling station that were used in GIS processes. Each record contained the averaged values for the physical/chemical parameters required by the three models. The final results for the three models were then exported in an appropriate format for importing into the GIS.

Dreissena Density – Landscape Feature Association

Part two of the study explored whether landscape features underlying and surrounding lakes could be used as predictors of *Dreissena* population density. We tested for associations between predicted *Dreissena* density (from the DFA-based density model) and various attributes of the landscape around and underlying lakes: (1) surficial (quaternary) deposits, (2) bedrock type, and (3) U.S. Environmental Protection Agency (USEPA) ecoregions. We used the categorical density model results, since they allowed straightforward classification of lakes and provided more information than simply absence versus presence.

The landscape feature datasets (layers) were also obtained from WDNR, along with a layer containing the Wisconsin state border (used to produce maps). The landscape features were represented spatially by polygons, along with an attribute that characterized the polygon. The landscape feature attribute data required aggregation from more detailed source data for surficial deposits and bedrock type.We used aggregate classifications that were developed as part of a state-wide groundwater contamination susceptibility analysis (Schmidt 1987). The purpose of these classifications was to determine the ability of surface contaminants to reach the water table. However, using data presented by Todd (1980), one can rank the bedrock and surficial deposits classes by calcium content. Since lake water calcium concentration is a factor in each of the models, and since it is expected that groundwater will generally have a significant impact on lake water chemistry, one could infer that potential colonization by zebra mussel is associated with the geologic structure surrounding a lake.

The ecoregion layer was originally derived by Omernik (1987). These continental-scale ecoregions are areas within which landscape ecology and other characteristics, such as weather, are thought to be similar. Omernik based his map of the coterminous 48 U.S. states on regional submaps of (1) land surface form, (2) potential natural vegetation, (3) land use, and (4) soils. Other maps were used to verify classification of land areas. Omernik et al. (1988) refined these ecoregions for the purposes of lake management based on soils, quaternary geology, bedrock, and phosphorus concentrations for inland lakes in Michigan, Minnesota, and Wisconsin. Omernik et al. (1991) then further refined the earlier mapping in a particularly problematic area, the northern west-central portion of Wisconsin. This final version was used in this study.

The model results from part one were first imported into the PC ARC/INFO GIS (version 3.4D, Environmental Systems Research Institute). Each layer within the GIS contained locational as well as attribute information. The lakes were located relative to their respective sampling stations's latitude/longitude coordinates and were considered as point locations for GIS analyses. These point coordinates were converted to the Wisconsin Transverse Mercator projection (a locally used alteration of the Universal Transverse Mercator coordinate system) so that overlays could be made with the other landscape layers that use this coordinate system. The attribute information for each lake included the result for each model.

The GIS analysis process consisted of performing a point-in-polygon overlay. In this procedure, the GIS overlaid the lakes, represented by their respective sampling location points, onto the landscape features, represented by polygons. A new attribute was then added to each lake that represented which landscape feature polygon the point (lake)

FIG. 2. Maps of predicted *Dreissena* density categories overlaid onto bedrock type, surficial deposits, and USEPA ecoregions. Crosses represent lakes where *Dreissena* are predicted to be absent (31 lakes). Squares represent lakes where *Dreissena* are predicted to be present in low densities (21 lakes). Triangles represent lakes where *Dreissena* are predicted to be present in high densities. (142 lakes).

Top: Bedrock types are (1) igneous, metamorphic, and volcanic, (2) sandstone, (3) carbonates, and (4) shale. Note that lakes predicted to be absent of *Dreissena* tend to be associated with the igneous/metamorphic/volcanic region. (Note that one lake was omitted due to missing data.) Middle: Surficial deposit types are (1) sand and gravel, (2) sandy, (3) peat, (4) loamy, and (5) clayey. Note that lakes predicted to be absent of *Dreissena* tend to be associated with gravel/sand and sandy areas. Bottom: Ecoregions are (1) western corn belt plains, (2) northern lakes and forests, (3) northern central hardwood forests, (4) driftless area, and (5) southeastern Wisconsin till plains. Note the paucity of lakes in the driftless area, and the near total association of lakes predicted to be absent of *Dreissena* in the northern lake and forest area.

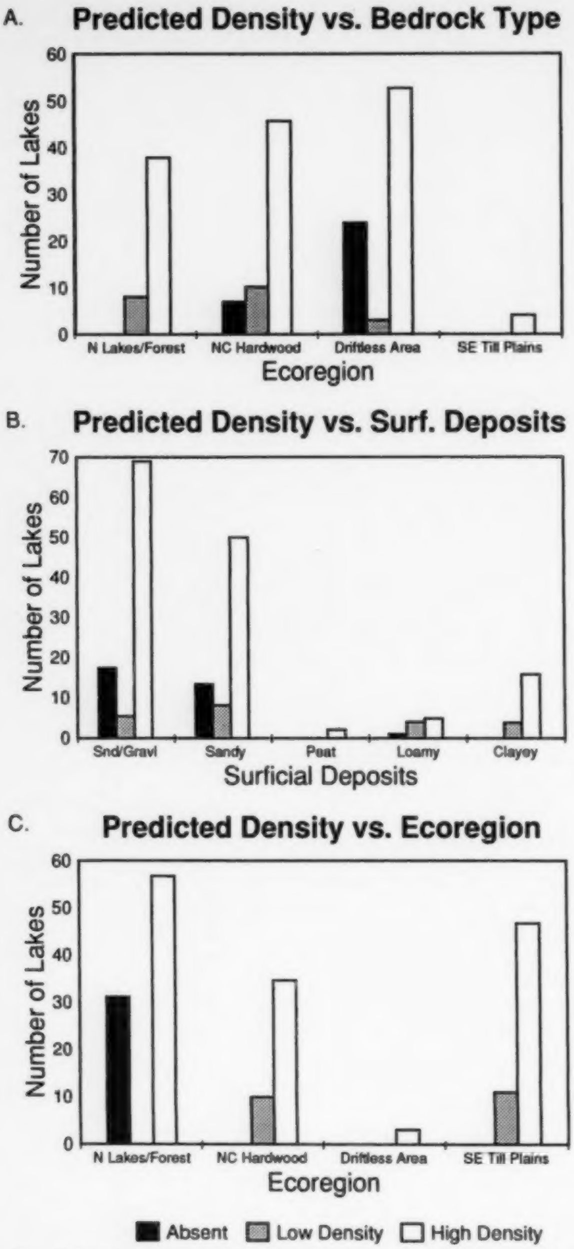

FIG. 3. (A) Histogram of predicted *Dreissena* density categories versus bedrock type. Note the association of absent lakes with igneous/metamorphic/volcanic and sandstone types. The association was statistically significant ($G = 34.9$, $p < 0.001$, df = 6). (B) Histogram of predicted *Dreissena* density categories versus surficial (quaternary) deposits. The density measure is absent, low density, or high density based on the second (discriminant function) model. Note the association of absent lakes with sand/gravel and sandy deposits. The association was statistically significant ($G = 18.4$, $p < 0.02$, df = 8). (C) Histogram of predicted *Dreissena* density categories versus USEPA-derived "ecoregions". Note that *all* the lakes predicted to be absent of *Dreissena* are located in the northern lakes and forests ecoregion. Ecoregions are northern lakes and forests, northern central hardwood forests, driftless area, and southeastern Wisconsin till plains. The western corn belt plains ecoregion contained no sample lakes. The association was statistically significant ($G = 77.5$, $p < 0.001$, df = 6).

fell into. This process was repeated for each of the three landscape feature layers. Final maps were produced with ArcView geographic inquiry and display software (version 1, Environmental Systems Research Institute).

Statistical associations between landscape characteristics and population density categories were tested using the G statistic (Legendre and Legendre 1983).

Results

The occurrence model produced a spatial concentration of lakes predicted to be absent of *Dreissena* in the northern part of Wisconsin (Fig. 1). Further, the density model indicated a spatial segregation of lakes predicted to have low *Dreissena* densities from those that would lack *Dreissena* (Fig. 1). The abundance model reinforced these patterns by indicating a gradient from lower to higher densities as one moves away from the north-central portion of Wisconsin (Fig. 1). All three models, however, suggest a broad distribution of lakes that are predicted to support *Dreissena* populations. (Note that southwestern Wisconsin was not under represented in the lake sample; this "driftless area" has very few lakes.)

A comparison of model results is shown in Table 2. The occurrence model predicted that *Dreissena* would be present in 47.9% of the lakes. In contrast, the density model predicted presence in 84.0% of the lakes and the abundance model 84.5%.

Part two of our study tested for association between various landscape features underlying lakes and *Dreissena* density class based on the density model. To illustrate the spatial relationship between the landscape features and the lakes, we produced a map for each landscape feature (Fig. 2). Landscape features were significantly associated with *Dreissena* density categories for each of the four landscape layers: (1) bedrock type ($G = 34.9$, $p < 0.001$, df = 6; Fig. 3), (2) surficial deposits ($G = 18.4$, $p < 0.02$, df = 8; Fig. 3), and (3) ecoregions ($G = 77.6$, $p < 0.001$, df = 6; Fig. 3). Low zebra mussel densities were associated mostly with the igneous/metamorphic/volcanic category of bedrock and sand-and-gravel or sandy surficial deposits.

Discussion

Our initial attempts to predict the spatial distribution of *Dreissena* among Wisconsin's inland lakes are encouraging. Earlier work by Neary and Leach (1992) looked at the potential for presence of *Dreissena* among a large sample of inland lakes in Ontario by using a GIS to map the results of threshold-based analysis of pH and calcium in those lakes. The pH and calcium threshold that they used were based on preliminary model results reported by C.W. Ramcharan, D.K. Padilla, and S.I. Dodson (Second International Zebra Mussel Conference). Our work used the three completed statistical models by Ramcharan et al. (1992) and available limnological data to predict absence or presence and population density of *Dreissena*. A GIS was used to test for associations between predicted lake population density classes and three landscape-scale characteristics. Overall, landscape-scale patterns appeared to be fairly consistent among the models, although they differ in details. Lakes without *Dreissena* were concentrated in the northern highlands, where forestry and tourism dominate. Calcium availability is probably the limiting factor. The lakes where lower densities of *Dreissena* were predicted are located mainly in the central and east-central portions of the state, which are dominated by agricultural use and some lesser urban centers. The densest populations of *Dreissena* were predicted in the south-central, south-eastern, and far western portions of the state. Here, urban/industrial and suburban areas are interlaced with agricultural areas. These areas have higher levels of available calcium from calcareous glacial till, and sandstone and carbonate bedrock. Further, due to agriculture, construction, and urban runoff, nutrient flow into these lakes is higher.

There was a noted disparity in the proportion of lakes where *Dreissena* were predicted to be absent versus present between the absence/presence only model and the two density model. For the Ramcharan et al. models, only lakes with known populations of *Dreissena* were used in development of their density and abundance models. In a test of their model, they found that no lakes with *Dreissena* were misclassified (as not supporting *Dreissena*), but there were some lakes without *Dreissena* that were misclassified as supporting *Dreissena*. Therefore, for the European dataset, the model seemed conservative. This may explain why there is an apparent difference in the absence/presence predictions using the density and abundance models (84.0% and 84.5% present, respectively) in comparison with the presence model (49.5% present). A more conservative approach would be to apply the presence/absence model first and then apply the density models to those lakes predicted to support *Dreissena*.

The variance among the models in the proportion of lakes predicted to have *Dreissena* present also reflects the relative uncertainty in model parameters developed by Ramcharan et al. (1992). In Fig. 4, one can see that many lakes are only marginally classified as absent versus present by the categorical density model. With small adjustments of the discriminant functions, many lakes would be reclassified: 51 lakes are located within ±20% of the absence/presence discrimination line. Further, shifting the focus to the occurrence model (a one-dimensional discriminant factor model), 52 of the lakes are within only ±10% of the absence versus presence discrimination value. Clearly, if parameters are refined the models could move into either lesser or greater agreement, but the potential exists to move them into greater agreement.

In part two of our study, the GIS provided spatial analytical capabilities that would have been impractical to implement manually. The results obtained here suggest that landscape features can potentially be used as a predictor for overall *Dreissena* distribution. More generally, this study suggests the potential for predicting general patterns of limnological characteristics of lakes across landscapes, based on the characteristics of the landscape itself.

On another level, this study demonstrates the relative ease with which ecological studies can be supplemented by use of a GIS as an analytical tool. Although our study used but a small subset of available GIS functionality, the results underscore the importance of looking beyond the spatial scales typically used in ecological studies. Frost et al. (1988) and Allen and Hoekstra (1992) provided strong arguments for looking at systems at spatial scales both larger and smaller than what experimental expediency might otherwise call for. They suggested that major insight can be gained by examining a system of multiple scales simultaneously.

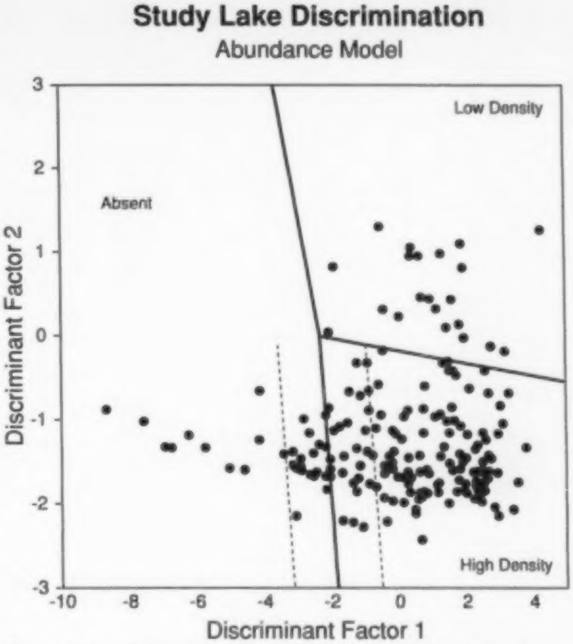

FIG. 4. Plot of the results from the DFA-based density category model. Note the number of lakes close to the absent/high-density discrimination line: 52 lakes were within a 20% variance band around the absent/high-density discrimination line.

Summary

We showed that the distribution of *Dreissena* populations and their densities are not likely to be uniform among Wisconsin inland lakes. We also showed that there is potential for using landscape scale features, associated with lake watersheds, to predict *Dreissena* density for lakes with less than adequate limnological data. This information will be valuable to resource managers, physical plant managers, and others.

However, this study does not address the timing of invasions for specific lakes or geographical areas (landscapes), nor how a population of zebra mussels in a given lake may be established over time. There are important questions to which future work needs to be directed.

Further research is required to lower the uncertainty in discriminating absence/presence in the Ramcharan et al. (1992) models. Ramcharan et al. used a relatively small set of lakes (76 lakes in the DFA occurrence model, 38 lakes in the DFA density model, and 58 lakes in the regression-based density model). The lake dataset used for their models does not include the complete range of limnetic factors in our Wisconsin lake dataset. A program of proactive study of inland water bodies invaded by *Dreissena* is needed to refine the Ramcharan et al. models for North American lakes. Enhancing the confidence of these models would allow for more robust individual lake predictions, as well as enhance the likelihood that the models could be used for management purposes.

Finally, future work should also look at more comprehensive landscape data. Such work should include (1) variability among landscape features for lake watersheds, (2) additional factors such as land use, and (3) lake inflow contribution volumes, i.e., surface water versus groundwater. It would then also be possible to assess whether these data can drive models to predict *Dreissena* occurrence in lakes for which inadequate limnological data exist, as the associations between landscape features and *Dreissena* occurrence demonstrated here suggest.

Acknowledgements

We would like to express our thanks to several who graciously reviewed this manuscript. The comments of Steve Ventura and Steve Adolph were particularly useful. Carol Tiegs, Don Ferber, and Lance Perry of WDNR provided invaluable access to needed survey data and GIS coverages. We would also like to thank the referees whose comments significantly improved the quality of the manuscript. D.K.P. would also like to thank the Director and Staff of the Friday Harbor Laboratories for providing access to computer facilities. This project was funded by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and the State of Wisconsin. Federal grant NA90AA-D-SG469 and grant NA16RG0531-01.

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Differential Predation by Northern Squawfish (*Ptychocheilus oregonensis*) on Live and Dead Juvenile Salmonids in the Bonneville Dam Tailrace (Columbia River)

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Petersen, J.H., D.M. Gadomski, and T.P. Poe. 1994. Differential predation by northern squawfish (*Ptychocheilus oregonensis*) on live and dead juvenile salmonids in the Bonneville Dam tailrace (Columbia River). Can. J. Fish. Aquat. Sci. 51: 1197–1204.

Juvenile salmonids (*Oncorhynchus* spp.) that have been killed or injured during dam passage may be highly vulnerable or preferred prey of predators that aggregate below dams. Salmonid loss due to predation will be overestimated using gut content analysis if some prey were dead or moribund when consumed. To examine this issue, field experiments were conducted in the Bonneville Dam tailrace (Columbia River) to compare rates of capture of live and dead juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*). Known numbers of coded-wire-tagged live and dead chinook salmon (*O. tshawytscha*) were released into the tailrace on six nights. Northern squawfish were collected after each release and their gut contents were examined for tags. When 50% of salmon released were dead, northern squawfish consumed 62% dead salmon. When 10% of salmon released were dead, comparable with dam passage mortality, 22% of the tags found in northern squawfish digestive tracts were from dead salmon. These results indicate that predator feeding behavior and prey condition are important considerations when estimating the impact of predation on a prey population.

Les salmonidés juvéniles (*Oncorhynchus* spp.) qui ont été blessés lors du passage d'un barrage peuvent être très vulnérables aux prédateurs qui se tiennent au pied des barrages ou constituer leurs proies favorites. La perte de salmonidés par prédation est surestimée lorsqu'on procède par analyse du contenu stomacal lorsque des proies mortes ou mourantes sont consommées. Pour examiner cette question, nous avons procédé à des expériences sur le terrain dans le canal de fuite du barrage Bonneville (fleuve Columbia) de manière à comparer les taux de capture de salmonidés juvéniles vivants et morts par la sauvagesse du nord (*Ptychocheilus oregonensis*). Des quinnats (*O. tshawytscha*) vivants et morts en nombres connus, et identifiés par des micromarques margnétisées codées, ont été jetés dans l'eau du canal de fuite au cours de six nuits. Nous avons capturé des sauvagesses du nord après chaque lâcher et nous avons retracé les micromarques dans le contenu stomacal. Lorsque 50 % des saumons relâchés étaient morts, le prédateur consommait 62 % de saumons morts. Lorsque 10 % seulement des saumons lâchés étaient morts, ce qui est comparable à la mortalité par passage dans le barrage, 22 % des micromarques trouvées dans le tractus digestif des sauvagesses du nord provenaient de saumons morts. On voit que le comportement d'alimentation du prédateur et que la condition des proies sont des facteurs importants pour l'estimation de l'impact de la prédation sur la population des proies.

Received April 21, 1993
Accepted November 25, 1993
(JB893)

Reçu le 21 avril 1993
Accepté le 25 novembre 1993

Estimating prey mortality due to a particular predator usually involves determining the capture rate or diet of the predator by analysis of gut contents (e.g., Rieman et al. 1991; Stewart and Ibarra 1991; Ruggerone and Rogers 1992). This approach may generate predation loss estimates that are too high, however, since the condition of prey (viable, moribund, or dead) when captured by a predator cannot be determined by examination of gut contents. Also, other sources of mortality may be underestimated if all prey observed in an opportunistic predator's gut are assumed to have died from "predation" whereas some prey may have died of starvation, disease, or other causes.

Northern squawfish (*Ptychocheilus oregonensis*) are major predators of juvenile salmonids (*Oncorhynchus* spp.) in the Columbia River, with salmonid losses being especially high in areas just downriver from dams (Petersen et al. 1990; Rieman et al. 1991; Shively et al. 1991). During 1983–86, 26–44% of the annual salmonid mortality in John Day Reservoir from northern squawfish predation occurred in the boat-restricted zone below McNary Dam, which is only 0.3% (0.6 km^2) of the total reservoir surface area (Rieman et al. 1991; J.H. Petersen, unpublished data). The boat-restricted zone is also an area where dead salmon are particularly numerous because of mortality caused by dam passage (Schoeneman et al. 1961; Long et al. 1975). Rieman et al. (1991) concluded that predation mortality of salmon in this area was greater than, or of similar magnitude to, mortality directly related to dam passage during April–July 1983–86. If predators eat significant numbers of dead salmonids, however, estimates of salmonid mortality due to predation may not be independent of dam passage mortality. Gadomski and Hall-Griswold (1992) demonstrated that north-

TABLE 1. Experiment dates, percent dead and live juvenile salmon released, river conditions, passage indices of preyfish, and northern squawfish consumption rates during six release experiments at Bonneville Dam. The salmonid passage index is a fish count expanded to river flow (data from the Fish Passage Center, Portland, Oreg.) whereas the American shad passage index is an unadjusted count of fish in the collection system (data from R. Martinson, National Marine Fisheries Service, Rufus, Oreg.). Consumption rate (mean prey per predator) is based on the number of CWT's or the total number of diagnostic bone counts in a northern squawfish digestive tract.

Release experiments				Conditions		Passage indices		Northern squawfish				
		Tagged salmon							Consumption (mean prey/predator)			
									Salmonids			
No.	Date	No. released	Dead:live (%)	River flow ($m^3 \cdot s^{-1}$)	Water temperature (°C)	Salmonids	American shad	Total catch	All	CWT	American shad	Percentage with one or more tags
1	27 Aug. 1990	5 095	52:48	4502	21.1	770	5794	398	0.3	0.2	1.0	8
2	28 Aug. 1990	3 056	57:43	4417	21.1	890	4715	253	0.3	0.1	1.2	8
3	27 Aug. 1991	10 000	10:90	3964	17	857	145	350	0.8	0.7	<0.1	25
4	29 Aug. 1991	10 000	50:50	3341	18	558	115	133	0.9	0.9	<0.1	20
5	3 Sept. 1991	10 000	50:50	3373	18	1035	114	130	1.1	0.9	<0.1	25
6	5 Sept. 1991	10 000	10:90	3143	17	508	131	127	0.5	0.4	<0.1	14

ern squawfish preferred dead over live juvenile chinook salmon (*O. tshawytscha*) in the laboratory, but the importance of dead prey in the field was not tested. In a river, complex water currents, turbidity, and other conditions not simulated in the laboratory might influence the number of dead prey encountered by northern squawfish and thus affect differential predation. The behavior of predators and prey may also differ in a field situation compared with observations in laboratory tanks.

The objective of this study was to compare the relative rates of capture of live and dead juvenile salmon by northern squawfish in a dam tailrace. Typically, field studies of selective foraging compare a measure of prey availability with diet data from predators (Ivlev 1961; Chesson 1978; Cock 1978; Pearre 1982). Using a prey availability measure to test preference, however, is especially difficult when predators and prey are highly mobile or prey have refuges (Zaret 1980). Assumptions must be made about the relative abundance and distribution of prey and predators, actual encounter frequencies, and individual versus group behavior. An alternative approach for testing preference in the field is to (1) tag different prey types, (2) release known numbers of tagged prey, (3) recover prey tags from the digestive tracts of predators, and (4) compare the frequencies of the prey types consumed. Hargreaves (1988) first used this approach and discussed the assumptions and advantages of releasing marked prey groups to test specific hypotheses. We adopted a similar experimental approach to examine differential predation on live and dead salmonids.

Methods

Prey Holding Conditions and Tagging

Prey were juvenile chinook salmon from the Little White Salmon National Fish Hatchery, Cook, Wash. Juvenile salmon for the 1990 experiments were held in 1400-L, 1.5-m-diameter circular tanks at the Columbia River Field Station (CRFS). Salmon for the 1991 experiments were held in hatchery raceways at Willard National Fish Hatchery, Cook, Wash. All tanks and raceways had flow-through well water at 7–8°C; salmon were fed a commercial diet of 2.5-mm moist pellets.

Juvenile salmon were tagged with binary-coded wire tags (CWT) (Jefferts et al. 1963) at least 25 d before release. CWT's have been used extensively on juvenile salmonids in the Columbia River Basin (e.g., Ebel et al. 1973; Wahle et al. 1981). Tag retention was ≥95% in all tagged groups except salmon tagged for Release 2, which had 60% (live group) and 72% (dead group) tag retention. Examination of fish from Release 2 (1990) indicated that tag loss was probably due to improper adjustment of the tagging machine.

Field Experiments

Two types of experiments were conducted. In the first experiment, live and dead salmon were equally abundant (50% dead and 50% live, called "50:50 releases"). In the second experiment, salmon were released in a live-to-dead ratio more typical of a dam tailrace zone (10% dead and 90% live, called "10:90 releases"). The 10:90 release experiment simulated a 10% dam passage mortality (e.g., Schoeneman et al. 1961). Four 50:50 releases and two 10:90 releases were conducted (Table 1). Experiments were done in 1990 and

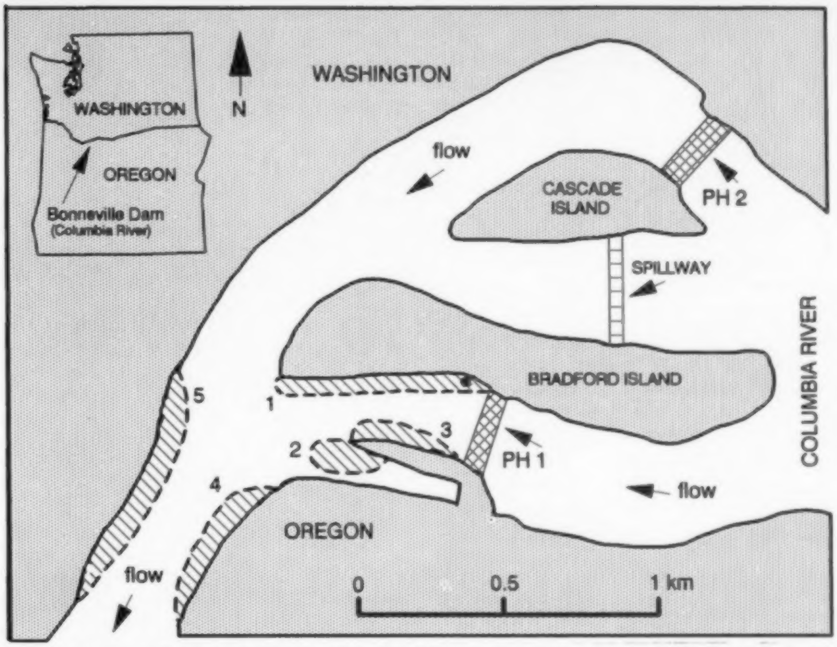

FIG. 1. Five sampling zones (1–5, diagonal hatching) for northern squawfish in the Bonneville Dam tailrace and location in Zone 1 (●) where tagged salmon were released. PH = Powerhouse.

1991 (Table 1) with procedures the same in both years except where noted. Results from 1990 releases were used in planning the 1991 experiments. Because chi-square sensitivity analyses (Elrod and Frank 1990) and tag return rates from 1990 indicated that releasing more fish would greatly improve the power of the statistical tests, releases in 1991 were about twice as large as releases in 1990.

We scheduled experiments during late August – early September to minimize the effects of naturally migrating salmonids and also to avoid possible interaction of alternate fish prey, especially juvenile American shad (*Alosa sapidissima*). Relatively few naturally migrating salmon are in the river during late August (since peak summer passage occurs in July), thus reducing the chance that our releases would be swamped by high densities of nonmarked salmon. Juvenile American shad migration does not usually peak until late fall. American shad density was, however, much higher during the 1990 releases than during 1991 (Table 1). The effect of the high density of juvenile American shad during the 1990 releases was considered during the analysis and interpretation of results.

Before release, salmon were acclimated to Columbia River temperature. In 1990, water temperature in holding tanks was increased about 1°C$\cdot$d^{-1} over a 10-d period to reach the river temperature of 21°C. Because salmon used in 1991 were held in hatchery raceways, maintenance water temperature could not be gradually increased. In 1991, fish were held in aerated 845-L transportation tanks and the temperature was gradually increased with flow-through heated water to 17.5°C over a 10-h period immediately prior to release.

On the day of a release experiment, two uniquely tagged groups of juvenile salmon were moved from the CRFS to Bonneville Dam in aerated, 114-L containers (maximum 500 fish per container) or aerated, 845-L transport tanks (maximum 5000 fish per tank). One group of salmon was killed immediately before release with a backpack electroshocker (900 V at 90 Hz for 20–30 s). Using electricity to kill salmon at the release site was efficient, rapid, and avoided potential problems such as predator avoidance that might be associated with the use of chemical poisons. Live and dead salmon were released through a fish transportation hose (about 20 cm in diameter) that emptied at the bypass outlet below Bonneville Dam Powerhouse 1 (Fig. 1). In 1990, alternating batches of live and dead salmon (about 500 fish per batch) were flushed through the transport hose; release of all fish required about 20 min. In 1991, live and dead fish were first mixed in one of the large transport tanks and all fish were released together. Most salmonids pass Columbia River dams at night (e.g., Brege et al. 1988), so all releases began at about 20:00 under dusk light conditions.

Sampling for northern squawfish was near shorelines in littoral and sublittoral habitats (<5 m) where they are most abundant (Nigro et al. 1985; Faler et al. 1988; U.S. Fish and Wildlife Service, unpublished data). Two 5.5-m electroshock boats were used to collect northern squawfish. Five areas ("zones") of the Bonneville Dam tailrace were selected for sampling, based on prior studies and accessibility (Fig. 1); Zones 2 and 3 were combined during the 1991 studies. Sampling effort was similar for all releases and was primarily along the south shore of Bradford Island (Zone 1), just downriver of the release site.

Collection of northern squawfish began 1 h after release of tagged juvenile salmonids and continued for about 9 h. The sampling period was limited so that tags ingested early in the evening would not be evacuated from the digestive tract before predator collection. Northern squawfish were killed onboard by a lethal dose of tricaine methanesulfonate

(MS 222) and returned to a processing site onshore within about 45 min of capture. Northern squawfish were measured (fork length (FL), nearest millimetre), and digestive tracts of all northern squawfish ≥250 mm FL were removed, placed in plastic bags, and preserved on ice. Digestive tracts of predators <250 mm FL were collected if they contained recently ingested salmon.

To recover tags, frozen samples of gut contents were thawed and processed in the laboratory using a digestive enzyme technique (Petersen et al. 1990). An enzyme solution (2% by weight, pancreatin and 1% sodium sulfide in lukewarm tap water) was mixed with gut contents in plastic bags and samples were held for 24 h in a 40°C desiccating oven. After all flesh was digested, the contents of each bag were agitated causing tags to settle to the bottom of the bag. Tags were collected, and samples were checked again using an electrical tag detector. The remaining contents were then rinsed through a 425-μm sieve with tap water, and diagnostic bones (primarily cleithra, dentaries, and opercles; Hansel et al. 1988) were removed. Diagnostic bones were identified and used to enumerate prey fish consumed. Binary codes on CWT's were read using a compound microscope.

Statistical Methods

Two analytical approaches were used. The first analysis tested whether the frequencies of live and dead salmon consumed by northern squawfish were different from release frequencies. Observed and expected frequencies of live and dead salmon captured were compared using chi-square analysis (Sokal and Rohlf 1981). Initial number tagged, percent tag retention, and posttagging mortalities were used to estimate the ratio of live and dead salmon released on a given day. Expected frequencies of live and dead salmon consumed for a day were based on the relative number of tagged salmon released in the two prey categories. Following the recommendation of Peterman (1990), the power $(1 - \beta)$ of a test was computed when the null hypothesis was not rejected $(\alpha > 0.05)$ using formulae from Sokal and Rohlf (1981) and Elrod and Frank (1990). Experimental results were also examined for heterogeneity.

For the second analysis, we explored the effect of various parameters on the proportion of dead salmon observed in individual predator digestive tracts. Analysis of covariance (ANCOVA) was used with the proportion of dead prey in each northern squawfish as the dependent variable (arcsine transformed using the method of Snedecor and Cochran 1980, p. 290). Independent variables in the analysis were northern squawfish FL (millimetres), the location where a predator was caught (Zone), release day, and the elapsed time (hours) between prey release and the time the predator was collected. Because of low predator catches and negligible tag returns in Zones 2, 3, and 4 on the Oregon shore, we combined these three zones for ANCOVA analyses.

Results

River Conditions

River flow and temperature were higher during the 1990 releases (Releases 1 and 2) compared with the 1991 releases (Releases 3–6; Table 1). In 1990, river flow was 4417–4502 $m^3 \cdot s^{-1}$ on release dates whereas flow was about 1000 $m^3 \cdot s^{-1}$ lower during the 1991 releases (Table 1). River temperature averaged 21°C during 1990 and 17.5°C during the 1991 release periods.

Northern Squawfish Catch and Diet

Catches of northern squawfish during the six release experiments ranged from 127 to 398, with a total of 1391 predators captured (Table 1). Most northern squawfish (46%) were caught in Zone 1 just downriver of the salmon release point (Fig. 1). About 16% (216 of 1391) of all northern squawfish collected contained at least one prey tag although this percentage was considerably higher during the 1991 experiments (Table 1).

Juvenile salmonids and juvenile American shad were the most common prey items. During the 1990 experiments, northern squawfish diet was 21% salmonids (percent occurrence of all prey fish), 78% American shad, and 1% other fish. During the 1991 experiments, northern squawfish diet was 94% salmonids, 5% American shad, and 1% other fish. Exoskeletons of crayfish (*Pacifasticus leniusculus*) were occasionally found in northern squawfish (<1% of total gut weight).

The greater proportion of juvenile American shad in the northern squawfish diet during 1990 was probably due to high numbers of American shad migrating downriver past Bonneville Dam during late August 1990 (Table 1). About 40 times as many American shad passed Bonneville Dam Powerhouse 1 during the 1990 release dates compared with the 1991 releases. Northern squawfish consumption of American shad (prey/predator; Table 1) was more than 10 times higher during 1990 compared with the 1991 rates.

Consumption of Live and Dead Salmon

Chi-square and covariance analyses were performed separately for the 50:50 and 10:90 experiments because of the different release ratios. The 50:50 dataset was further subdivided by year, 1990 versus 1991, because of the higher release numbers in 1991 (Table 1), annual temperature differences, and the possible effects of abundant juvenile American shad in 1990 (Table 1).

Released salmon averaged 92 mm FL ($N = 300$; SD = 7 mm). Mean FL of salmon was not significantly different among the six release experiments (ANOVA, $P > 0.25$) or between paired live and dead batches (*t*-tests, $P > 0.25$).

For the four nights when salmon releases were 50:50, northern squawfish contained 62% (205) tags from dead salmon and 38% (125) tags from live salmon (Table 2). Frequencies of tags recovered from live and dead salmon were significantly different from expected frequencies during the first 1990 experiment but not during Release 2; total, pooled, and heterogeneity chi-squares were not significant in 1990 (Table 2). During 1991, the first 50:50 release had about equal numbers of live and dead prey consumed whereas significantly ($P < 0.001$) more dead salmonids were eaten on the second night (Release 5; Table 2). The high number of tags from dead salmon eaten during Release 5 (86) caused the total and pooled chi-squares to be significantly different from expected (Table 2).

When 10% of the released salmon were dead, 22% (58) of the tags recovered were from dead prey (Table 2). Total and pooled frequencies were significantly different from the expected 10:90 release ratio, but between-day heterogeneity was also significant (Table 2). For Release 6, only 32 tags

TABLE 2. Numbers of observed and expected tags recovered from northern squawfish digestive tracts during six release experiments. Expected number of tags is based on release proportions of live and dead salmon (see Table 1). *P* is the probability that observed and expected frequencies are significantly different (*$P < 0.05$; ***$P < 0.001$; NS, $P > 0.05$).

Release No.	Tags from live salmon		Tags from dead salmon				
	Observed	Expected	Observed	Expected	Chi-square	df	*P*
			50% dead – 50% live releases, 1990				
1	27	36.2[a]	48	38.8[a]	4.5	1	*
2	13	12.9[a]	17	17.1[a]	0.0	1	NS
Total	40	48.8	65	56.6	4.5[b]	2	NS
Pooled					2.7	1	NS
Heterogeneity					1.8	1	NS
			50% dead – 50% live releases, 1991				
4	52	53.0	54	53.0	0.0	1	NS
5	33	59.5	86	59.5	23.6	1	***
Total	85	112.5	140	112.5	23.6[b]	2	***
Pooled					13.4	1	***
Heterogeneity					10.2	1	***
			10% dead – 90% live releases, 1991				
3	179	212.4	57	23.6	39.3	1	***
6	31	28.8	1	3.2	2.2	1	NS
Total	210	241.2	58	26.8	41.5[b]	2	***
Pooled					31.4	1	***
Heterogeneity					10.1	1	***

[a] Expected numbers differ slightly from a 50:50 ratio because the dead-to-live ratio was not 50:50 for Releases 1 and 2 (see Table 1).

[b] Summation of chi-square statistics from separate releases.

were recovered from northern squawfish, and the expected and observed frequencies were not different (Table 2). For the other 10:90 release (Release 3; Table 2), however, 236 tags were recovered and the observed frequency of tags from dead salmon was significantly greater than the expected frequency.

Tag recoveries from three releases (Releases 2, 4, and 6) were not significantly different from expectation ($\alpha > 0.05$; Table 2), so the null hypothesis that predation was proportional to the ratio of live and dead salmon released could not be rejected for these releases. However, the power ($1 - \beta$) of these individual chi-square tests to detect a significant change from expectation was low ($1 - \beta < 0.60$; power calculation was not relevant when the null hypothesis was rejected, see Peterman 1990).

Of the three covariance analyses, overall models were not significant for the 10:90 releases ($P > 0.68$; df 5,96) or for the 50:50 releases during 1990 ($P > 0.12$; df 5,46). The overall ANCOVA model for the 50:50 releases from 1991 was significant ($P < 0.05$; df 5,53; $r^2 = 29\%$), with time of northern squawfish capture ($P < 0.001$) and zone ($P < 0.03$) being significant independent variables. In the 50:50 releases from 1991, the proportion of tags from dead salmon found within northern squawfish increased rapidly with time after release (Fig. 2). During the first 2 h after salmon were released the proportion of dead prey in northern squawfish digestive tracts was less than expected (Fig. 2), but this proportion increased rapidly during the next 2-h period and then remained high (Fig. 2). In the 50:50 releases during 1991, the proportion of dead prey in predator digestive tracts was significantly higher in Zone 1 near the release point (0.57 dead) than in Zone 5 about 1 km downriver (0.35 dead; Fig. 1).

Discussion

Few data are available on the occurrence of dead prey in the diets of fishes. Indeed, many predators prefer live prey, using movement as a feeding cue (Ware 1973; Howick and O'Brien 1983; Irvine and Northcote 1983; Luczkovich 1988). Northern squawfish, however, consumed many dead salmon in the Bonneville Dam tailrace, and for three of six releases, significantly more dead than live juvenile chinook salmon were eaten than was expected from the release proportions. When 10% of salmon released were dead, similar to estimated passage mortality at Columbia River dams, 22% of the tags found in northern squawfish digestive tracts were from dead salmon. When 50% of released salmon were dead, 62% of recovered tags were from dead prey.

Our feeding experiments in the Bonneville Dam tailrace corroborated laboratory studies where northern squawfish were offered live and dead juvenile chinook salmon (Gadomski and Hall-Griswold 1992). Similar to our field results, Gadomski and Hall-Griswold (1992) found that northern squawfish selected dead salmon more often than expected from the original stocking proportion. When 50% of available salmon were live and 50% dead, 67% of all salmon eaten by northern squawfish in the laboratory were

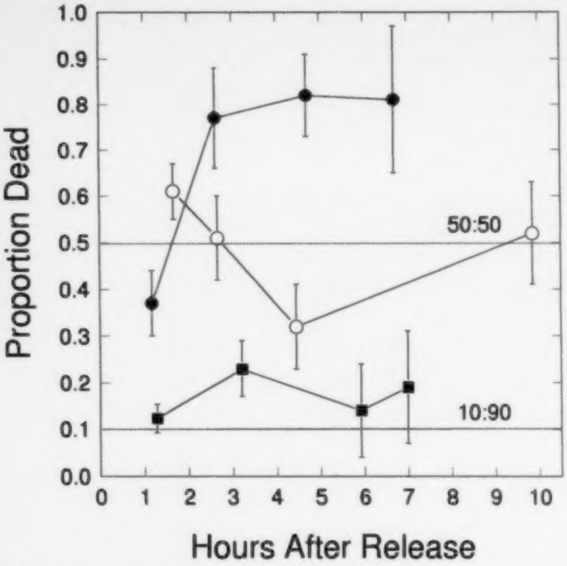

FIG. 2. Proportion of tags from dead salmon (mean, SE) recovered from northern squawfish collected following release of live and dead juvenile salmon. The mean collection time was computed for intervals of 0–2, 2–4, 4–6, and >6 h. Results are shown for the 50% dead releases (1990, ○; 1991, ●) and the 10% dead releases (1991, ■).

from the dead group compared with 62% dead salmon consumed in the present study. Also similar to our field results, northern squawfish in the laboratory ate a higher than expected proportion of dead salmon when only 20% of the offered salmon were dead (Gadomski and Hall-Griswold 1992).

Day-to-day heterogeneity in live and dead capture proportions (Table 2) may have been caused by small sample sizes on some nights. The capture proportions of live and dead salmon did not differ from expectation on three of six individual nights; however, two of the three nights having nonsignificant results also had the smallest numbers of recovered tags ($N = 30$, $N = 32$). In Release 4, an intermediate number of tags were recovered ($N = 106$), but the proportion of live to dead prey was almost exactly the same as the release proportion (Table 2). Chi-square values from individual nights were positively correlated with the number of tags recovered ($r = 0.90$; $P < 0.02$), also indicating a strong sample-size effect.

Heterogeneity may also have been influenced by experiment timing. When release and capture proportions of dead salmon were not significantly different from expected (Releases 2, 4, and 6), another experiment (Releases 1, 3, and 5, respectively) had been performed 1–2 d earlier (Table 1). All experiments that showed significant selection of dead prey were conducted following at least four nights with no electroshock or boat activity in the tailrace. Repeated electroshocking has been shown to affect fish feeding behavior (Mesa and Schreck 1989), catchability (Cross and Stott 1975; Yundt 1983), and physiological condition (Schreck et al. 1976; Mesa and Schreck 1989), although no such studies have been done with northern squawfish. The total catch of predators in our study also declined considerably between Releases 1 and 2 (398 and 253 northern squawfish, respectively) and between Releases 3 and 4 (350 and 133 northern squawfish, respectively), suggesting some depletion of the local population.

Although northern squawfish consumed more dead salmon than expected, we cannot necessarily conclude that northern squawfish actively selected or preferred dead over live prey. Rather than testing for predator choice per se, our experiments quantified the effective predation rates on live versus dead fish in a field situation. Differential predation could have been caused by a number of factors other than predator choice. For example, the behavior of live chinook salmon or the drift patterns of dead salmon may have caused differential availability of the two groups in the Bonneville Dam tailrace. Live and dead salmon should have been adequately mixed when prey were released, but turbulence and flow patterns in the Bonneville Dam tailrace might have caused dead salmon to settle in areas with low water velocity, which are also preferred by northern squawfish (Faler et al. 1988). Giorgi et al. (1988) released live and dead chinook salmon with radio-tags below the Lower Granite Dam (Snake River) and monitored passage of tagged fish at three downriver stations. Live and dead chinook salmon that eventually passed a station 6.1 km downriver of release had median residence times of 3 and 10 h, respectively (Giorgi et al. 1988). A longer residence time for dead salmon in the Lower Granite (or Bonneville) Dam tailrace would increase their exposure to northern squawfish predation. Live salmon, on the other hand, may have swum rapidly out of the tailrace areas. Live salmon might also seek refuge among rocks or cobble (Chapman and Bjornn 1969), thus reducing their vulnerability to northern squawfish predators.

Physical trauma, pressure changes, and gas supersaturation cause juvenile salmonid deaths during dam passage, whether fish migrate through a bypass system, through turbines, or over a spillway. Direct estimates of turbine- or spill-related mortality have been highly variable (Eicher Associates, Inc. 1987; Bell 1990; Cada 1990), and methods to measure this mortality continue to be refined (Heisey et al. 1992). At Lower Monumental Dam on the Snake River, Long et al. (1975) estimated that 11–28% of juvenile coho salmon (*O. kisutch*) died during passage through a turbine. At McNary Dam on the Columbia River, Schoeneman et al. (1961) estimated turbine and spillway mortality to be 11 and 2%, respectively. Total mortality of fish passing a Columbia River dam depends on species, fish size, turbine design, guidance efficiency of the bypass system (if present), operating conditions, and other factors (Schoeneman et al. 1961; Eicher Associates, Inc. 1987; Bell 1990).

The results of our experiments suggest that predation loss estimates in dam tailrace areas may be too high because of the occurrence of dead salmon in these areas. Assuming 10% dead and 90% live salmon in a dam tailrace on the Columbia River (e.g., Schoeneman et al. 1961), the actual loss of live salmonids to predation in this area would be about 22% less than has been estimated. In the McNary Dam boat-restricted zone during 1983–86, for example, about 0.12 million of the estimated 0.55 million juvenile salmonids annually consumed by northern squawfish (Rieman et al. 1991) could have been dead when ingested. If total salmonid mortality from dam passage is greater than 10% and northern squawfish are eating many dead fish, the impact of local predators might be seriously overestimated using an uncorrected loss estimate. Revised loss estimates could alter management strategies by directing efforts and resources to those areas where salmonid mortalities are highest.

Estimates of predation loss for river reaches distant from dams may also be sensitive to nonpredation sources of salmon mortality if predators opportunistically feed on dead or dying prey. Rieman et al. (1991) estimated that 78% of all predation mortality in John Day Reservoir occurred downriver of the McNary Dam boat-restricted zone. Such mortality estimates for midreservoir areas would be too high if some of the salmon recovered from northern squawfish were dead when ingested. Disease, starvation, and gas supersaturation are possible sources of salmonid mortality away from dams (Ebel 1977; Raymond 1979; Leong and Barilla 1983), although specific estimates of nonpredation mortality factors do not exist for midreservoir areas. Some salmon killed during dam passage could also drift into the midreservoir area and be consumed. Following release just below Lower Granite Dam, 7% of dead radio-tagged salmon drifted at least 6 km downriver (Giorgi et al. 1988). Possible consumption of dead salmonids by northern squawfish, combined with our poor understanding of other sources of juvenile salmon mortality, makes predation loss estimates in midreservoir areas especially difficult.

Acknowledgments

Dave Jepsen and Roger Tabor were especially helpful with sample processing and data analyses. Conrad Frost, Milton Hunter, Matt Mesa, Alice Murphy, R.D. Nelle, Todd Olson, Sally Sauter, and Rip Shively helped with field and laboratory work, which we appreciate. The U.S. Army Corps of Engineers, particularly Jim Kuskie, provided access and assistance at Bonneville Dam. Bill Nelson, Greg Ruggerone, and Kurt Fresh made constructive comments that significantly improved the manuscript. This work was funded by a contract with the Bonneville Power Administration (DE-AI79-88BP91964) that was administered by Bill Maslen.

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Comparative Pharmacokinetics and Bioavailability of Oxolinic Acid in Channel Catfish (*Ictalurus punctatus*) and Rainbow Trout (*Oncorhynchus mykiss*)

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Kleinow, K.M., H.H. Jarboe, K.E. Shoemaker, and K.J. Greenless. 1994. Comparative pharmacokinetics and bioavailability of oxolinic acid in channel catfish (*Ictalurus punctatus*) and rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. 51: 1205–1211.

The pharmacokinetics, bioavailability, and disposition of oxolinic acid (OA), a quinolone antibacterial drug, were examined in a warmwater (channel catfish (*Ictalurus punctatus*)) and coldwater fish species (rainbow trout (*Oncorhynchus mykiss*)). Studies were performed at 24 and 14°C for catfish and at 14°C for trout to compare temperature- and species-related differences. Analysis of OA pharmacokinetics when determined by HPLC provided elimination half-life ($t^1/2_\beta$), volume of distribution (V_{ss}), and clearance (Cl_b) estimates for 24°C catfish, 14°C catfish, and 14°C trout of 40.9, 69.3, and 81.3 h, 939, 880, and 1817 mL/kg, and 16.3, 8.9, and 16.9 $mL \cdot kg^{-1} \cdot h^{-1}$, respectively. Following oral administration, OA plasma concentrations peaked between 8 and 24 h for all treatments; however, 14°C trout and 14°C catfish sustained peak concentrations for a longer duration than 24°C catfish. Oral OA bioavailabilities were 56.0, 91.8, and 90.7% for 24°C catfish, 14°C catfish, and 14°C trout, respectively. OA distribution data for muscle of 14°C catfish demonstrated an inordinately high peak concentration and delayed time to peak relative to other treatments. Elimination half-lives of OA in muscle were 33.1, 54.3, and 141 h for 24°C catfish, 14°C catfish, and 14°C trout, respectively.

On a évalué la pharmacocinétique, la biodisponibilité et l'élimination de l'acide oxolinique (AO), une quinolone aux propriétés antibactériennes, chez des espèces de poisson d'eau chaude (barbue de rivière (*Ictalurus punctatus*)) et d'eau froide (truite arc-en-ciel (*Oncorhynchus mykiss*)). Les études se sont déroulées à 24 et 14 °C avec la barbue et à 14 °C avec la truite, de manière à permettre la comparaison des différences en fonction de la température et des espèces. Déterminée par CLHP, la pharmacocinétique de l'AO se lit comme suit : demi-vie d'élimination ($t^1/2_\beta$), volume de distribution (V_{ss}) et clearance (Cl_b) chez la barbue à 24 °C, chez la barbue à 14 °C et chez la truite à 14 °C : 40,9, 69,3 et 81,3 h, 939, 880 et 1 817 mL/kg et 16,3, 8,9 et 16,9 $mL \cdot kg^{-1} \cdot h^{-1}$, respectivement. Suite à une administration orale, on observe que la concentration plasmatique de l'AO atteint un sommet après 8 à 24 h dans tous les cas; toutefois, la truite à 14 °C et la barbue à 14 °C ont gardé une concentration de pointe plus longtemps que la barbue à 24 °C. La biodisponibilité de l'AO administré par voie orale est de 56,0, 91,8 et 90,7 % chez la barbue à 24 °C, chez la barbue à 14 °C et chez la truite à 14 °C, respectivement. Les données sur la distribution de l'AO dans les tissus musculaires de la barbue à 14 °C montrent une concentration de pointe anormalement élevée et un délai anormalement prolongé avant l'atteinte de la concentration de pointe, relativement aux autres traitements. La demi-vie d'élimination de l'AO dans le tissu musculaire a été de 33,1, 54,3 et 141 h chez la barbue à 24 °C, chez la barbue à 14 °C et chez la truite à 14 °C, respectivement.

Received April 26, 1993
Accepted November 25, 1993
(JB897)

Reçu le 26 avril 1993
Accepté le 25 novembre 1993

Oxolinic acid (5-ethyl-5,8-dihydro-8-oxo-1,3-dioxolo-[4,5-*g*]quinoline-7-carboxylic acid) (OA), a member of the 4-quinolone series of antibiotics, is thought to be effective in controlling bacteria by in part interfering with DNA gyrase (Tsoumas et al. 1989). As a chemotherapeutic agent, this drug has been used to control gram-negative bacterial urinary infections in man (Madsen and Rhodes 1971) and other mammals (Ziv 1976). Recently, OA has been used in Europe and Japan for the control of bacterial epizootics in food fish (Endo et al. 1973a, 1973b; Steffenak et al. 1991). Efficacy has been demonstrated for the control of the fish pathogens *Aeromonas hydrophila, A. liquefaciens, A. salmonicida, Chondrococcus columnaris, Vibrio anguillarium*, and *Yersinia ruckeri* (Endo et al. 1973a; Archimbault et al. 1988).

Numerous studies have addressed issues related to OA residues (Kasuga et al. 1984; Endo et al. 1987; Archimbault et al. 1988; Ueno et al. 1988; Jacobsen 1989) as well as the influence of environmental parameters such as pH, salin-

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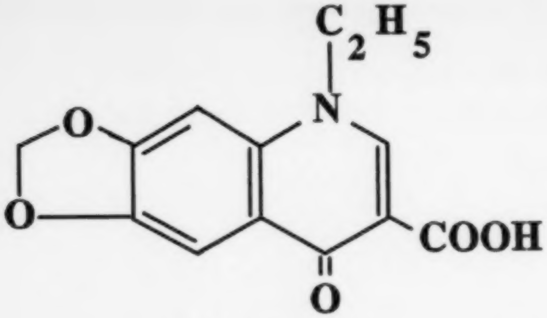

FIG. 1. Structure of OA.

ity, and temperature on OA pharmacokinetics in fish (Endo and Onozawa 1987a, 1987b). While it appears to be well established that the extent of OA accumulation can be species specific (Kasuga et al. 1984; Ueno et al. 1988), the relationship of environmental temperature to OA retention remains ill defined. Studies with OA in rainbow trout (*Oncorhynchus mykiss*) have demonstrated no relationship (Jacobsen 1989), an inverse relationship (Ueno et al. 1988), and a direct relationship of residue elimination to temperature (Kasuga et al. 1984).

The purpose of the present study was twofold: (1) to describe the kinetics, bioavailability, distribution, and fate of OA in an as yet uncharacterized aquaculture species, the channel catfish (*Ictalurus punctatus*), and (2) to compare calculated parameters obtained under identical conditions (of sampling, dosing, and analysis) in rainbow trout held at 14°C and channel catfish held at 14°C and 24°C. Three major experiments, single-dose pharmacokinetics, oral bioavailabilty, and tissue distribution, were performed for each of these treatment groups. These studies ascertained species differences and temperature effects on the disposition of OA.

Materials and Methods

Animals

Rainbow trout (602–1268 g) were obtained from Greers Ferry National Fish Hatchery, Heber Springs, Ark. Channel catfish (450–1114 g) were acquired from the LSU Aquaculture Research Station, Baton Rouge, La. The fish for all treatment groups were maintained under flow-through conditions in dechlorinated tap water (pH 7.9 ± 0.5; total hardness 26.5 ± 1.0 mg $CaCO_3$/L; alkalinity 176.0 ± 2.0 mg $CaCO_3$/L) on a 12 h dark : 12 h light photoperiod. Catfish were divided into two separate groups, one held at 24°C (preferred acclimation temperature) and the other at 14°C. All trout were held at 14°C (preferred acclimation temperature). All fish were maintained under these conditions for at least 4 wk prior to the experiments. Fish were fed Silver Cup® trout chow (Murray Elevators, Murray, Utah) on a daily basis up to the day prior to surgical preparation or experimentation.

Chemicals and Reagents

OA was obtained from Argent Chemical Company (Redmond, Wash.) (Fig. 1). The sodium salt was formed from the parent acid by stoichiometric addition of 1.0 N NaOH. Chemical purity (99.8%) was verified by liquid chromatography following purification over silica gel. Nalidixic and piromidic acids used as analytical internal standards were purchased from the Sigma Chemical Company (St. Louis, Mo.). All other reagents were of the highest quality commercially available.

Sampling Methods and Surgical Procedures

The fish used for i.v. and oral pharmacokinetic/bioavailability studies were held individually during experiments in flow-through chambers that facilitated the use of aortic cannulas and indwelling stomach tubes in free-swimming fish (Kleinow 1991). Administration of OA intravenously or by gavage and access for sequential blood sampling were facilitated by this system.

For cannula and stomach tube implants, tricaine methanesulfonate (Argent Laboratories, Redmond, Wash.) was used for induction and maintenance of anesthesia. Dosages for anesthetic induction and maintenance in trout were 90 and 40 mg/L, respectively, and 140 and 70 mg/L, respectively, in catfish. After anesthetization, fish were allowed a minimum of 24 h before experimentation. Studies in trout suggest that this is adequate time for clearance of anesthetic, reestablishment of normal renal function (Hunn and Willford 1970), and recovery of cytochrome P-450 activity (Fabacher 1982; Kleinow et al. 1986).

Pharmacokinetics

OA as the sodium salt was dissolved in 0.9% saline and administered as a single i.v. dose (5 mg/kg) via an aortic cannula to each member of the three treatment groups. These groups consisting of seven fish each included trout at 14°C (798 ± 222 g body weight), catfish at 14°C (622 ± 127 g), and catfish at 24°C (812 ± 181 g). Blood samples (~750 μL) were collected via aortic cannulae for all groups at 3, 5, 10, and 20 min and at 1, 4, 8, 24, 48, 72, 96, 120, and 144 h postdosage. In addition, blood samples were collected at 168 h for trout and 168 and 192 h for 14°C catfish. Parent compound in the plasma was determined by HPLC analysis.

Oral Bioavailability

Six fish for each of the three experimental treatment groups (14°C trout (868 ± 94 g), 14°C catfish (852 ± 218 g), and 24°C catfish (668 ± 24 g)) were dosed with OA (5 mg/kg) via gavage for the purpose of examining bioavailability and oral pharmacokinetics. The dose consisting of the appropriate amount of OA for each individual animal was mixed in a 2-mL slurry of maintenance diet. The dose was followed by a 2-mL chaser of dietary slurry to ensure delivery from the stomach tube. Following dosing, blood (~500 μL) was collected via aortic cannulae from the three treatment groups at 0.5, 1, 4, 8, 12, 16, 20, 24, 28, 36, 48, 72, 96, 120, 144, and 168 h. Blood was also collected from 14°C catfish at 192, 216, 240, 268, and 288 h. Samples were analyzed by HPLC.

Tissue Distribution

The distribution of OA into muscle and bile was determined for each of the three treatment groups (14°C trout (302 ± 56 g), 14°C catfish (404 ± 75 g), and 24°C catfish (391 ± 66 g)). A total of 72 animals divided into three equal-sized groups were administered sodium OA (5 mg/kg) in a maintenance diet slurry mixture. Four animals for each treatment were sampled at 24, 48, 72, 96, and 120 h. Additional muscle and bile samples were collected from 24°C catfish at 168 h and from the other treatments at 240 h. Tissues were extracted and analyzed as described under HPLC methods. The half-lives ($t^{1}/2_{\beta}$) of OA in muscle and bile were calculated using linear regression of postabsorption data. Residue half-life determinations were performed according to $t^{1}/2 = 0.693/\lambda$ where λ is the slope of the fitted data.

HPLC Analyses of Oxolinic Acid

Blood samples were centrifuged at 12 000 rpm (13 000 *g*) for 5 min. Resulting plasma samples (500 μL) were vortexed, sonicated, and extracted with 10 mL of acetonitrile using the procedures of Hamamoto (1986). Muscle tissues were extracted for OA using matrix solid-phase dispersion (MSPD) according to the methods of Jarboe and Kleinow (1992). Briefly, this procedure involves blending 0.5 g of finely chopped muscle into 2.0 g of octadecyl silica gel (C_{18}) (Analytichem International, Harbor City, Calif.) with a glass pestle until the sample mixture appears homogenous. The resulting matrix is packed into columns whereby OA is successively eluted with hexane (8 mL), acetonitrile (8 mL), and methanol (8 mL). Bile (50 μL), following precipitation with a saturated NaCl salt solution (1950 μL), was exhaustively extracted with ethyl acetate (8 mL) (mean extraction efficiency 82.8%). Following extraction, all resulting fractions were concentrated to dryness and stored (−14°C) under nitrogen in the dark until analysis.

HPLC analyses of OA were performed on an Alltech Versapack® C_{18} reverse-phase column maintained at 40°C. For measurement of OA concentrations in plasma, a 6:7:1, methanol/0.1 M citric acid/acetonitrile mobile phase was used under isocratic conditions (Hamamoto 1986) (Fig. 2A). OA from bile and muscle extractions was chromatographed under stepped gradient conditions (50 min) consisting of 100% 0.05 M acetic acid (AA) for the first 5 min followed by a 35-min period of a 2%/min increase in methanol to 70% methanol/30% AA. These conditions were maintained for 5 min before increasing to 100% methanol over the last 5 min (Fig. 2B). Authentic OA standards were used as retention standards on a daily basis. Quantification of OA was accomplished using a standard curve constructed on the basis of an extracted compound/internal standard ratio. Areas under the curve (AUCs) were used for formulation of analyte/internal standard comparisons. Selection of the internal standard varied with chromatographic conditions. Nalidixic acid was used as an internal standard for plasma samples and piromidic acid for bile and muscle.

Pharmacokinetic Analysis

OA plasma concentration data resulting from i.v. and oral dose administration were modeled following fitting using PCNONLIN 4.0 software (Statistical Consultants, Inc., Lexington, Ky.). Subsequent pharmacokinetic analyses were performed according to statistical moment theory (Gibaldi and Perrier 1982).

Oral bioavailability was determined with the areas under the respective i.v. and gavage plasma concentration – time curves for each treatment as described by

$$\frac{\mathrm{Dose}_{\mathrm{i.v.}} \times \mathrm{Auc}_{\mathrm{oral}}}{\mathrm{Dose}_{\mathrm{oral}} \times \mathrm{AUC}_{\mathrm{i.v.}}} \times 100.$$

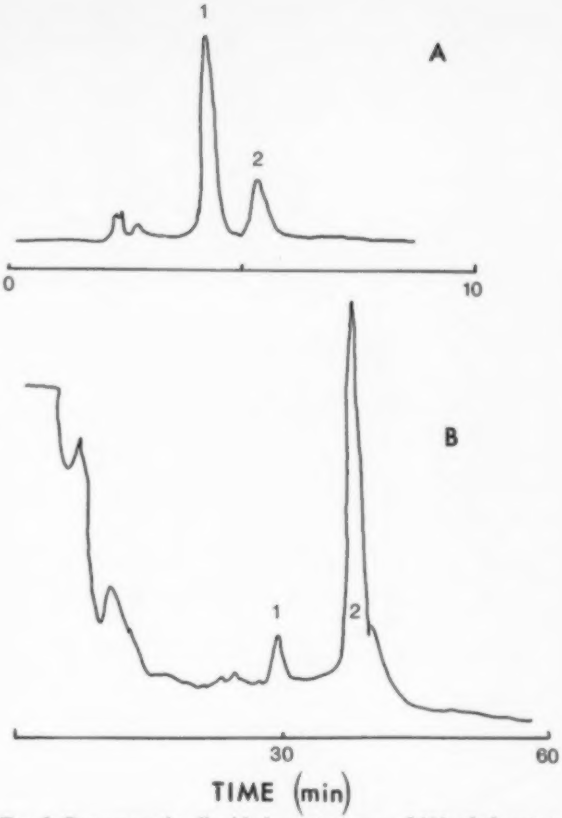

FIG. 2. Representative liquid chromatograms of (A) ethyl acetate extracted plasma sample from 24°C catfish 5 min following i.v. administration (plasma contained incurred oxolinic acid (1) and 3.0 μg of nalidixic acid (2) as the internal standard) and (B) MSPD-extracted muscle sample from 24°C catfish 48 h following oral administration (muscle contained incurred oxolinic acid (1) and 2.5 μg of piromidic acid (2) as the internal standard).

The AUC was estimated by the equation

$$\mathrm{AUC} = \int_0^{\infty} C_{\mathrm{pd}}\, t$$

where *C* was the plasma drug concentration at time *t*. The AUC from $t = 0$ to time of last measured concentration (t^*) was calculated according to Simpson's rule. The AUC from t^* to infinity was estimated by C^*/λ_z where C^* was the concentration at t^* and λ_z was the elimination rate constant calculated as −2.303 multiplied by the slope of the terminal phase of the log plasma concentration versus time curve.

Statistics

All statistical comparisons were performed with a one-way ANOVA or the Student *t*-test (Sokal and Rohlf 1973). Variables were considered significantly different at $P \leq 0.05$. Data are presented as mean ± SD.

Results and Discussion

Mean plasma OA concentrations following a single i.v. administration (5 mg/kg) to 14°C trout, 14°C catfish, and 24°C catfish are plotted in Fig. 3. Drug disappearance from

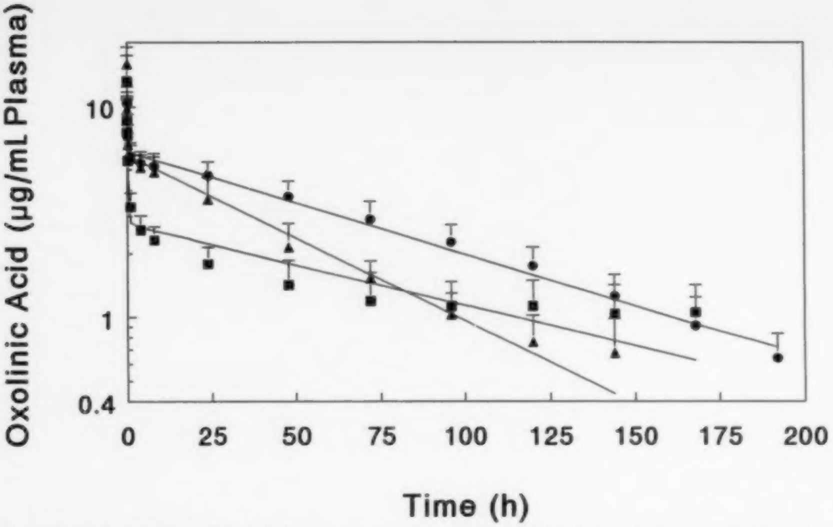

FIG. 3. Semilog plot of plasma OA concentration versus time following a single i.v. administration of OA (5 mg/kg) to catfish at 24°C (▲), catfish at 14°C (●), and trout at 14°C (■) ($N = 7$ for each treatment). All points are means ± SD. Line represents model-predicted values.

TABLE 1. Pharmacokinetic values (means ± SD) in rainbow trout (14°C) and channel catfish (14 and 24°C) following a single i.v. administration of OA (5 mg/kg). $t^1/2_\alpha$ = biological half-life of OA in plasma during distributional phase; $t^1/2_\beta$ = biological half-life of OA in plasma during the elimination phase of the drug; V_{ss} = apparent steady-state volume of distribution; Cl_b = whole-body clearance rate; Cl_t = intercompartmental clearance rate. $N = 7$ for each temperature and species treatment. For individual parameters, values followed by the same letter are significantly different at $P \leq 0.05$.

Parameter	Trout (14°C)	Catfish (24°C)	Catfish (14°C)
$t^1/2_\alpha$ (h)	0.15 ± 0.09	0.032 ± 0.017	0.68 ± 0.84
$t^1/2_\beta$ (h)	81.3 ± 22.5 a	40.9 ± 7.9 ab	69.3 ± 6.9 b
V_{ss} (mL/kg)	1817 ± 219 ab	939 ± 192 a	880 ± 128 b
Cl_b ($\mathrm{mL{\cdot}kg^{-1}{\cdot}h^{-1}}$)	16.9 ± 5.8 a	16.3 ± 3.7 b	8.9 ± 1.7 ab
Cl_t ($\mathrm{mL{\cdot}kg^{-1}{\cdot}h^{-1}}$)	1714.6 ± 925.4	2372.9 ± 1069.1	1095.7 ± 1389.5

plasma was biexponential for all experimental treatments. Trout exhibited a more precipitous decline in OA concentrations during the alpha distribution phase and a more gradual beta phase elimination compared with catfish acclimated at either 14 or 24°C. Intertreatment differences were reflected in the calculated pharmacokinetic parameters for the three treatments as listed in Table 1.

Species differences in OA pharmacokinetics were ascertained with trout–catfish comparisons at the same temperature (14°C) and at temperatures reflecting optimal conditions for each species. These comparisons suggest that at 14°C, trout and catfish differ significantly in regard to the volume of distribution (V_{ss}) and whole-body clearance rates (Cl_b) of OA. Trout at 14°C and catfish at 24°C exhibited similar Cl_b but differed significantly in $t^1/2_\beta$ and V_{ss}. Under all conditions of comparison, trout exhibited significantly larger calculated V_{ss}. The similarity of V_{ss} between 14 and 24°C catfish coupled with the uniform difference between either group of catfish and trout suggests that V_{ss} is a major species difference irrespective of acclimation temperature for the catfish. These findings may be attributed to processes including drug sequestration, vascular perfusion, membrane permeability, and depot composition.

Temperature-related differences between catfish acclimated at 14 and 24°C were reflected in Cl_b and $t^1/2_\beta$. Significant differences in Cl_b were evident, with values of 8.9 and 16.3 $\mathrm{mL{\cdot}kg^{-1}{\cdot}h^{-1}}$ at 14 and 24°C, respectively. Intercompartmental clearances (Cl_t) were highly variable, especially among the 14°C catfish. Under all comparisons, however, Cl_b rather than Cl_t appears to control the rate of elimination of the drug. Mean plasma $t^1/2_\beta$ were significantly longer for the 14°C (69.3 h) than for the 24°C (40.9 h) acclimated catfish. These values were inversely related to clearance. A variety of factors may account for this temperture-dependent relationship such as cardiac output (Randall 1970), bile excretion rates (Curtis et al. 1986), membrane lipid composition (Hazel 1984), and xenobiotic biotransformation (reviewed in Kleinow et al. 1987).

Several published studies have examined the pharmacokinetics of OA in salmonids following i.v. administration (Björklund and Bylund 1991; Hustvedt and Salte 1991; Hustvedt et al. 1991b). These studies have incorporated a

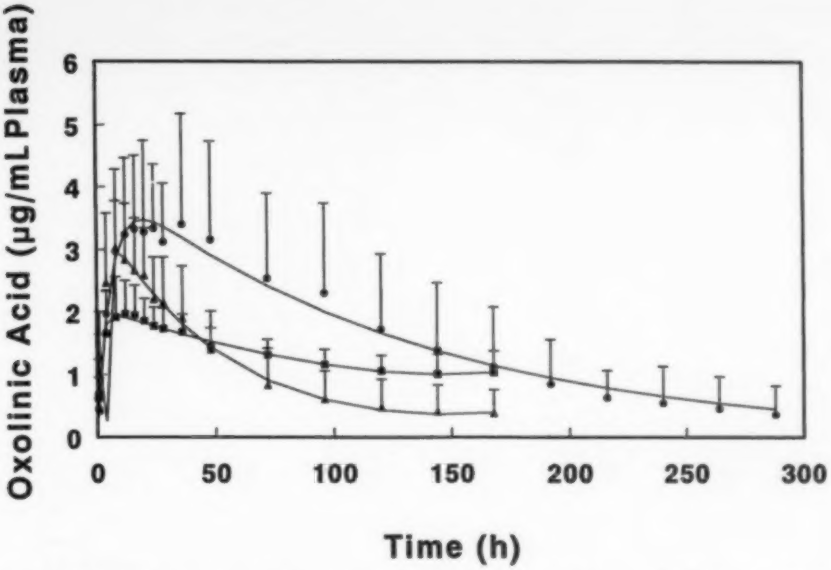

FIG. 4. Plasma OA concentration versus time following oral administration of OA (5 mg/kg) to catfish at 24°C (▲), catfish at 14°C (●), and trout at 14°C (■) ($N = 6$ for each treatment). All points are means ± SD. Line represents model-predicted values.

range of dosages (5–20 mg/kg), different temperatures (8.5–16°C), and a variety of administration/holding/sampling techniques (cannulated, noncannulated, restrained, nonrestrained). While the variety of experimental protocols makes direct comparisons suspect, many values in our current study correlate well with those of Björklund and Bylund (1991). The $t^{1}/2_{\beta}$, V_{ss}, and Cl_b for the Björklund and Bylund (1991) study were 69.7 h, 1900 mL/kg, and 20.2 mL·kg^{-1}·h^{-1}, respectively. These values compare with $t^{1}/2_{\beta}$, V_{ss}, and Cl_b estimates in the current study of 81.3 h, 1817 mL/kg, and 16.9 mL·kg^{-1}·h^{-1}. Values presented for trout at 8.5°C (Hustvedt and Salte 1991) and Atlantic salmon (*Salmo salar*) at 9.0°C (Hustvedt et al. 1991b) varied more substantially with V_{ss} and Cl_b values in trout of 2900 mL/kg and 50 mL·kg^{-1}·h^{-1} (Hustvedt and Salte 1991), respectively. Sampling techniques (Kleinow 1991) and temperature (Björklund et al. 1992), variables in these comparisons, have been shown to alter drug pharmacokinetic parameters in fish.

Following oral administration, the time course of absorption and elimination, as well as the magnitude of peak OA concentrations in plasma, varied markedly among the three treatment groups (Fig. 4). Peak plasma concentrations in catfish at both 24°C (3.09 µg/mL) and 14°C (3.71 µg/mL) were greater than those in trout (2.07 µg/mL). Peak concentrations appeared early in the sampling regime for all temperature and species combinations, with peak concentrations occurring at 8, 12, and 24 h for 24°C catfish, 14°C trout, and 14°C catfish, respectively. While 24°C catfish demonstrated the shortest time to peak, 14°C catfish and 14°C trout demonstrated the most persistent OA concentrations. This latter relationship was similar to that observed following i.v. administrations.

Peak OA concentrations in trout (2.07 µg/mL) following oral administration were in the same general range as reported elsewhere for salmonids, despite large differences among studies with regard to dosage. Other studies in which trout were orally administered OA at dosages ranging from 40 to 75 mg/kg reported serum or blood concentrations from 2.0 to 5.2 µg/mL (Ueno et al. 1988; Björklund and Bylund 1991; Björklund et al. 1992). Similarly, Atlantic salmon demonstrated peak serum concentrations from 1.7 to 2.5 µg/mL (Hustvedt et al. 1991a, 1991b). High apparent OA bioavailabilities in the current study may, in part, account for the similarity in reported peak OA concentrations.

Bioavailability of OA following oral administration to 24°C catfish, 14°C catfish, and 14°C trout was 56.0, 91.8, and 90.7%, respectively. Although there are no published bioavailability values for OA in catfish and mammals, our values for trout are considerably higher than those previously reported for trout (13.6–38.1%) (Cravedi et al. 1987; Björklund and Bylund 1991) and Atlantic salmon (20–25%) (Hustvedt et al. 1991a, 1991b). As a point of further comparison, the value reported here for trout is comparable with mammalian values published for the closely related quinolone, nalidixic acid (Harvey 1975). Procedural differences between the current study and cited salmonid papers, with regard to carrier vehicle, ionization of the drug, and dose of OA administration, may account in part for these discrepancies. Björklund and Bylund (1991) and Hustvedt et al. (1991b) administered OA as an aqueous suspension at dosages of 75 and 10 mg/kg, respectively. In contrast, we administered OA as the sodium salt at 5 mg/kg in a fish diet slurry. Apparent bioavailabilities of xenobiotics have been reported to be altered by chemical form (Kleinow et al. 1992), particle size (Endo et al. 1987), and dietary lipid content (Vetter et al. 1985) in fish, as well as by dosage and carrier vehicle in mammals (Winter 1988).

Temperature-related differences in bioavailability between 14°C (91.8%) and 24°C (56.0%) acclimated catfish may be the result of the relative rates of intestinal evacuation. It has been demonstrated in a variety of fish species that intestinal clearance rates decrease substantially with lower temperatures (Shrable et al. 1969; Windell et al. 1976). This

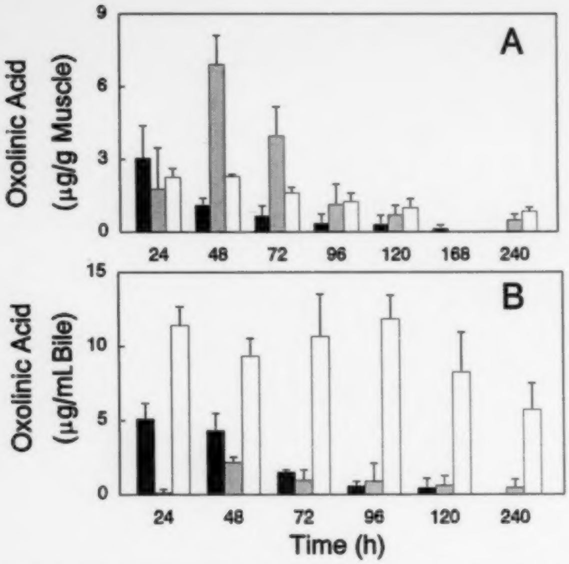

FIG. 5. (A) Muscle and (B) bile OA concentration versus time following oral administration of OA (5 mg/kg) to catfish at 24°C (■), catfish at 14°C (▤), and trout at 14°C (□) (*N* = 4 for each treatment at each data point). All points are means ± SD.

effect could increase absorptive contact time for those drugs and matrices in which bioavailability is limited primarily by transit time rather than chemical form (Winter 1988) or blood flow.

Data on muscle OA distribution following oral administration are shown in Fig. 5A. Catfish at 14°C showed the highest OA muscle concentrations among the three treatments for the times sampled. Terminal elimination half-lives were 33.1, 54.3 and 141 h for 24°C catfish, 14°C catfish, and 14°C trout, respectively. OA elimination rates from catfish muscle were inversely related to temperature. This relationship is consistent with studies in trout by Ueno et al. (1988) and Björklund et al. (1992). Equivocal results, however, have been presented for trout muscle with inverse (Ueno et al. 1988; Björklund et al. 1992), direct (Kasuga et al. 1984), and independent (Jacobsen 1989) OA residue to temperature relationships reported.

Following oral administration, 14°C catfish exhibited plasma OA concentrations that were 40–50% higher than those of 24°C catfish at the 24- and 48-h samplings (Fig. 4). This relationship was not evident in muscle, where 14°C catfish exhibited lower OA concentrations than 24°C catfish at 24 h and an almost sevenfold higher level at 48 h. These findings indicate a time delay to peak muscle concentrations in 14°C catfish. In addition, changes in muscle concentrations for 14°C catfish were not proportional to changes in plasma concentrations during the same interval. In contrast, the 24°C catfish and 14°C trout exhibited plasma/muscle OA concentrations that followed closely throughout the time course. These results suggest that perfusion or transport of OA into the muscle of 14°C catfish may be rate limited. Likewise, the elevated muscle OA concentrations of 14°C catfish at later samplings (relative to 24°C catfish) may reflect the slow clearance rates and perhaps a temperature-related sequestration.

OA concentrations in the bile are shown in Fig. 5B. Trout demonstrated the highest OA concentrations followed by the 24°C catfish and 14°C catfish, respectively. While trout exhibited sustained OA levels in bile throughout the time course, 24°C catfish demonstrated a transient peak concentration at 24 h. In contrast, a delay to peak (48 h) was observed for the 14°C catfish. The high OA concentrations sequestered in trout bile as compared with catfish may contribute to the greater apparent volume of distribution observed for trout (Table 1).

These studies have demonstrated that OA pharmacokinetics and disposition vary with both the fish species and acclimation temperature. OA clearance, elimination half-lives, oral bioavailability, as well as distribution into muscle and bile were temperature dependent in the catfish. The major species difference when compared at the same and divergent temperatures was the volume of distribution. In general, trout exhibited longer $t_{1/2\beta}$ and larger V_{ss} values than their catfish counterparts. Clinically, these findings suggest that compared with 14°C catfish or 14°C trout, 24°C catfish will require higher OA dosages and/or shorter dosing intervals for maintenance of a therapeutic blood concentration. Likewise, extended drug withdrawal times will be necessary for either species at 14°C compared with 24°C catfish.

Acknowledgements

Funds for this research were provided to K. Kleinow under FDA grant No. U01 FD 01466. The authors would like to thank B.R. Toth, J.R. Griggs, and M.A. Gentry for their laboratory assistance. Additionally, we wish to thank the personnel of Greers Ferry National Fish Hatchery and the Ben Hur Aquaculture Research facility for providing research fish.

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

MULTIFAN: Estimation of Growth Parameters

Fournier et al. (1990) proposed a new method for estimating growth parameters and age composition from multiple length frequency data sets. The new method referred to as the MULTIFAN model aims to extend the previous existing methods such as ELEFAN and those by Schnute and Fournier (1980), Fournier and Breen (1983), and Sparre (1987). Fournier et al. (1990) took account of two types of deviations: (a) deviations caused by occurrence of rare events and (b) larger deviation than expected, i.e., the frequency observed in a length interval is either much higher or much lower than it should be. They intended to develop a likelihood-based estimation that is robust or insensitive to the two types of deviations from the model. They started by assuming a normal density for $\tilde{Q}_{i\alpha}$ (the proportion of fish in the αth length frequency data set having a length lying in the length interval i) and then modifying the density form twice in order to obtain the desired robustness.

As is known, the likelihood measures the possibility of the observed events under the statistical model adopted. When the model fits the data poorly, we would expect biased estimates. To obtain more reliable estimates, it is preferable to revise the statistical model (and hence obtain a different likelihood function) rather than change the likelihood. It is reasonable to modify the likelihood function subjectively to obtain robustness. However, this may result in (1) bias in the estimation and (2) unreliable statistical inference when the inference is based on the likelihood such as significance test for model selection. On the other hand, when the likelihood function (the "true" model) is known, one may modify the likelihood or the score function to reduce the bias in the estimation (e.g., Firth 1993). Apart from the philosophical aspects about the principle of modelling, I have three more concerns about the MULTIFAN model.

(1) The observed range of $Q_{i\alpha}$ is always between 0 and 1, as it is a proportion. For a normal density, its range is $(-\infty, +\infty)$. Therefore, assuming a normal density for $\tilde{Q}_{i\alpha}$ is inappropriate, especially when $Q_{i\alpha}$ is near 0 or 1. It often happens that $Q_{i\alpha}$ are small.

(2) Obviously, $\sum_i \tilde{Q}_{i\alpha} = 1$. Therefore, as noticed by the authors, the mutual independence of $\tilde{Q}_{i\alpha}$ is not true.

(3) The likelihood function (equation 2.2) that is used for final estimation is in fact not a proper density function.

One of the important advantages of using a maximum likelihood approach is that the estimates are consistent (asymptotically unbiased) under some conditions. However, it is not known whether the MULTIFAN retains this property or not? When $f_{i\alpha}$ is assumed to be a multinomial distribution, maximizing the likelihood is equivalent to minimizing the separation statistic A defined in equation 1.3. It seems possible to obtain the desired robustness by modifying A. For example, if we assume that a fish can be classified randomly to any one of the length classes with a small probability, say, $1/N_I$, we will have

$$\mathbf{E}(Q_{i\alpha}) = (N_I - 1)\xi_{i\alpha}/N_I + 1/N_I^2.$$

The estimation will be robust to the type I deviation, possibly the type II deviation as well — YouGan Wang, *IPPP Biometrics Unit, CSIRO, Division of Fisheries, P.O. Box 120, Cleveland, Qld. 4163, Australia.* (JC312)

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Response to Wang

Wang has expressed several reservations about the statistical methods employed in our MULTIFAN model. While we feel that his concerns are unfounded, they may be shared by other workers, so we would like to take this opportunity to discuss them.

Wang states, "To obtain more reliable estimates, it is preferable to revise the statistical model (and hence obtain a different likelihood function) rather than change the likelihood."

But this is exactly what we have done! We have emphasized modifications to the likelihood function in the discussion because the calculations used for parameter estimation are based on the likelihood function. However, each modification to the likelihood function corresponds to a modification of the statistical model.

Wang suggests that some results of Firth (1993) can be used instead of our approach. But Firth assumed that he already had the correct statistical model, i.e., the likelihood function.

Wang suggests that bias could be removed by employing the multinomial likelihood function with Firth's bias-removing procedure. However, it is clear that the multinomial likelihood function is not adequate for describing many of the real length frequency data sets which occur. For example, it commonly occurs that the mean length of the fish in an age class is significantly larger or smaller than the model predicts. Thus the entire mode corresponding to this age class will be shifted to the left or right. The multinomial model is not robust with respect to these deviations, and the addition of a small number to the expected values occurring in each age class as Wang suggests will not make it so.

We feel that Wang has overlooked a most important point. The main necessity for adopting a robust likelihood function such as the one we use in MULTIFAN is so that we could perform significance tests to compare different model hypotheses. Significance tests are used to select the "correct" model to fit the data, for example, deciding how many significant age classes are represented in the data. Significance tests are important in length frequency analysis because one commonly finds that the estimated values of the parameters of interest depend on the model selected. This influence is probably considerably larger than any bias associated with a particular likelihood function.

Wang notes that since the quantities $Q_{i\alpha}$, must satisfy the constraints $0 \leq Q_{i\alpha} \leq 1$, they are not normally distributed. This is true, but it is only of great importance when the $Q_{i\alpha}$ have values near the bounds, i.e., close to 0 or 1. For fisheries data, it seldom happens that all the fish lie in one length interval (in this case, there is little information in the data anyway). Our methods have already removed most of the influence of the observations for the case when the $Q_{i\alpha}$ take on values close to 0, so the skewed distribution of the $Q_{i\alpha}$ does not play a large role.

Wang notes that the expression (2.2) is not a proper density function. While this is true, it is still the case that the estimates we use are maximum likelihood estimates. The reason for this is that we do not maximize the likelihood function with respect to the parameter δ. Rather, we set δ equal to 0.5 times the estimate of the variance that one would get for normally distributed errors, i.e., the mean squared deviations. This technique for "tuning" the amount of robustness is discussed more fully in Otter Research Ltd. (1993, chap. 12).

Finally, MULTIFAN is a commercial product which must work with real data. The parameter estimation and hypothesis testing procedures were developed by using MULTIFAN on a large number of data sets for animals with very different life histories. Our goal was to obtain a consistent methodology which would require a minimum amount of subjective turning by the user. The results of some of these investigations are described in Fournier et al. (1990, 1991) and Labelle et al. (1993). In addition, we have extended this methodology to an age-structured model for the analysis of catch at length data for exploited fisheries. Terceiro et al. (1992) have done simulations comparing MULTIFAN with a different method of length frequency analysis — D.A. Fournier and J.R. Sibert, *Otter Research Ltd., P.O. Box 265, Station A, Nanaimo, BC V9R 5K9, Canada.* (JC155)

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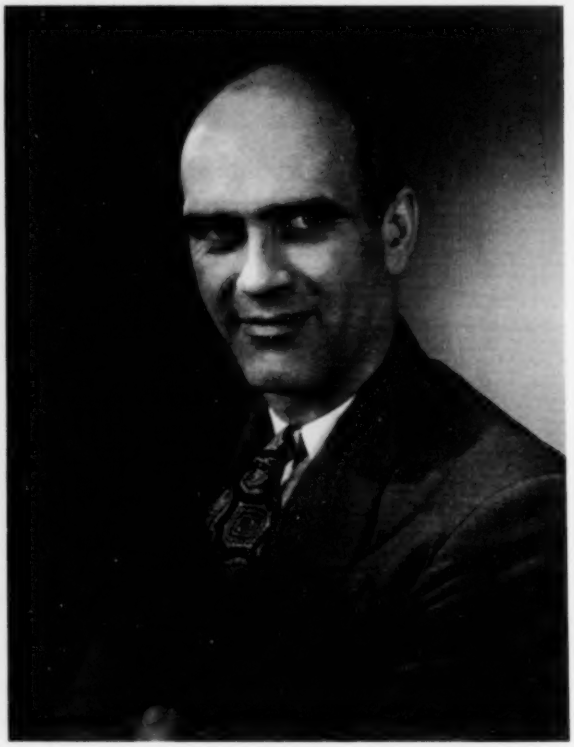
OBITUARY/NÉCROLOGIE

William Membery Sprules

1916–1994



Bill Sprules, internationally known fishery scientist and administrator, died on January 12, 1994, in Ottawa. He was best known as a Canadian commissioner or delegate on several international fisheries commissions.

Bill was born in Hamilton, Ontario, on December 28, 1916. His naturalist life-style began with cottage life in that area. During his education as an honours student in high school, and in Trinity College, he received many awards for his athletic achievements in track and rugby. He loved playing jazz as a piano player in local bands.

At the University of Toronto, he enrolled in honour biology and developed a special interest in the aquatic ecosystems program at the Ontario Fisheries Research Laboratory, which was newly relocated in Algonquin Park. During the summers of 1938–41, he participated in the overall program and specialized in the ecology of stream insects. He received a B.A. degree in 1939 and a Ph.D. degree in 1942. His first scientific paper "The effect of a beaver dam on the insect fauna of a trout stream" was published in 1940. His doctorate thesis "An ecological investigation of stream insects in Algonquin Park", published in 1947, received international interest. It provided comparative data for an acidification study carried out almost five decades later, 1984–85.

During the war years, 1942–44, Bill was a meteorological officer with the British Commonwealth Training Schools, primarily at the Royal Canadian Air Force Station in Dunnville, Ontario.

From 1944 to 1949, he was a biologist with the Fisheries Research Board of Canada at the Central Fisheries Research Station in Winnipeg. He participated in an experimental management study of Heming Lake and investigations of sea-run trout, Arctic char, and belugas along western Hudson Bay. Throughout this period, his primary interest was the life history and management requirements for Winnipeg goldeye. The main results of this research were published in a Bulletin entitled "Goldeye in Canada" by Kennedy and Sprules (1967). The keen interest that he acquired in the Canadian Arctic continued throughout his life.

In 1949, Bill moved to London, Ontario, as Associate Professor of Zoology at the University of Western Ontario. He was well-liked by his students for the professionalism and collegiality of his lectures. As part of his teaching and research responsibilities, he was director of a fisheries and limnology field station on Lake Erie. He collaborated with Helen Battle of that university in a publication on the unique pelagic eggs and early development of the goldeye (1960).

In 1951, Bill was appointed Chief of the Fish Culture Development Branch of the Department of Fisheries in Ottawa. He was responsible for the fish hatchery program and for salmon and trout enhancement. In 1954, he was promoted to Assistant Director of Conservation and Development, with broader responsibilities for conservation and enhancement of various fisheries. Such appointments of research scientists to administrative positions were relatively new in the Department. They proved to be useful in dispelling some feelings of incompatability between administration and research.

During the years 1946–53, there were increasing international concerns, investigations, and negotiations concerning the serious impact of parasitic sea lampreys in the upper Great Lakes. Dr. Sprules participated in the process leading to a Convention in 1954 and a Great Lakes Fishery Commission in 1956. During this period, he devoted many weekends of fieldwork to the development of the Canadian role in an international program to control lampreys. The resultant electrical barrier program, which was partially successful in the 1950's, was superseded by a chemical lampricide program initiated by the Great Lakes Fishery Commission in 1958.

Early in 1957, he became Special Assistant to the Deputy Minister of Fisheries to provide scientific advice and assist with development of policy. His expertise was especially valued at international fishery commission meetings. This led to his appointments as Canadian Commissioner on three of these commissions (International Pacific Halibut Commission, 1960, North Pacific Fur Seal Commission, 1961, and International Whaling Commission, 1963). His scientific background and negotiating capabilities were highly respected and he served Canada well.

In 1965, Bill became Director of the International Fisheries Service. With a very small staff, he was responsible for the development and negotiation of Canadian positions for a great variety of international fisheries matters, such as extended jurisdiction, salmon interception, and all of Canada's involvement with international fishery commissions. In his roles as commissioner and staff support to other Canadian commissioners (e.g., International North Pacific Fisheries Commission), he travelled extensively. His international achievements were recognized with an Honorary Key to the City from the Governor of Hokkaido, Japan, and a Canadian Centennial Medal (1967).

During 1964–69, he served as a member of the Fisheries Research Board of Canada. He contributed to a shift in Board policy from emphasis on fish species of major commercial importance to biological aspects of limnology and oceanography and strengthened ties with Canadian universities. As a member of an International Joint Commission Board, he had a special interest in a growing problem of eutrophication in the Great Lakes. He was influential in the decision that the Fisheries Research Board was best qualified to do the relevant research. Accordingly, a Freshwater Institute was established on the campus of the University of Manitoba, replacing the Central Fisheries Research Station in London, Ontario. Laboratory research, manipulation of small lakes, and Great Lakes monitoring led to an effective program of eutrophication control. Similar changes of research direction took place on the Atlantic and Pacific coasts.

After retiring in 1973, Bill enjoyed two decades of family life. He and Jean, a very devoted couple, celebrated their fiftieth wedding anniversary in 1992 and enjoyed their close relationship with children Gary, Nancy, and Robbie and their families. Bill made creative use of his hands and pursued his interests as a naturalist at their trailer and cottage sites. His continuing interest in stamp collecting contributed to his enviable knowledge of global geography. His athletic interests focussed on professional baseball, and he maintained an active participation in a fisheries poker club.

In summary, Bill Sprules was a proud Canadian and an exemplary achiever. He fostered the importance of ecosystem science and international collaboration for the understanding and management of our living aquatic environment.

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CJFSDX51(5)985-1215 (1994)
ISSN 0706-652X

Canada

Printed in Canada by / Imprimé au Canada par
University of Toronto Press, Inc.
Typesetting by / Typographie par
Aubut & Nadeau Services Inc.

0706-652X(199405)51:5;1-C